duction. Just as the magnetic permeability of iron is not constant, but varies with the magnetic force acting on it, so the conductivity of metallic particles is not constant, but varies with the E. M. F. acting on them. The characteristic curves given above bear also a remarkable resemblance to the curves of magnetisation. Other parallelisms will be noted later. These similarities are probably due to the fact that in both cases we are dealing ultimately with phenomena of molecular deflection and rearrangement, taking place in one, under increasing magnetising force, and in the other, under increasing electromotive force.

As the absolute values of the current and the E. M. F. are known, it is easy to find the resistance of the receiver for any given E. M. F. The different values of the resistance can also be determined by the *method of substitution*. After the curve is drawn, leaving the paper still on the platform, a resistance box is substituted for the receiver, and the whole operation is repeated, with this difference, that now we have to change the resistance continuously in order to keep the galvanometer spot on the curve. The values of these resistances at definite points of the curve now correspond to the resistances of the receiver at those points. We can thus find the value of the resistance of the receiver at any point in the curve. This way of finding the resistance was used to supplement that of direct calculation $\left(R=\frac{E}{C}\right)$, from the known values of the E. M. F. and the corresponding current; the two results were found practically identical.

I give below a table showing the variation of resistance with E. M. F. for the curve A (fig. 52).

Table I.—Showing the Variation of Resistance with E. M. F.

E. M. F. (volt).	Current (in 1/10^5 amps)	Resistance (ohms).
0·05	2·0	2,500
0·10	4·1	2,440
0·15	6·6	2,270
0·20	9·2	2,100
0·25	14·0	1,770
0·30	20·0	1,500
0·35	28·5	1,230
0·40	44·6	860
0·45	69·0	640

It will be seen from the above table that as the E. M. F. increased from 0·05 volt to 0·45 volt the resistance decreased continuously from 2,500 to 640 ohms, *i.e.*, about one-fourth its original value, and *this diminution of resistance or increase of conductivity is not abrupt, but continuous.*

In the lower portion of the curve, where the E. M. F. is low, the resistance is great and its variation small; but the curve soon becomes steep with the rise of the electromotive force. With a higher E. M. F. the change, to which the conductivity variation is due, proceeds very rapidly. This change is so great that at a certain critical value of E. M. F. it is almost abrupt. This is well seen in curve A, a little beyond 0·45 volt.

When the E. M. F. is adjusted to fall just short of the critical point, say, at 0·4 volt, then a slight increase of E. M. F., say +0·1 volt, will cause a very great variation of current; whereas if the E. M. F. had been so adjusted as to fall very much below the critical point, say, at 0·3 volt, an additional electromotive force of the same amount 0·1 volt, produces a relatively small variation of current. In the former case, conditions stood as it were on the brink of a precipice, and a slight additional impetus precipitated a fall. It will thus be seen that if the E. M. F. acting on the receiver be so adjusted as to be near the critical point, a slight electromotive variation will produce a great change, exhibited by a very considerable increase of conductivity. It is interesting to note in this connection that I found the sensitiveness of receivers to electric radiation could be greatly enhanced by raising the E. M. F. acting on the circuit to a point as high as they could bear, just short of electric instability.

Influence of Intensity of Initial Current in Modifying the Characteristic Curve

When at the beginning of an experiment the receiver is adjusted at a definite low E. M. F., say, 0·05 volt, we can have any initial current, according to the adjusted pressure of contact, the current increasing with increase of pressure. We may thus start with a large or a small initial current, the E. M. F. at starting being constant.

In the curve B (fig. 52) the initial current is a little more than double that for A. It will be seen that the curve has become distinctly steeper; the critical point is at the same time lowered, from 0·46 volt as in the last case, to 0·43 volt. The sudden bend in the curve is now less pronounced. In connection with the lowering of the critical point by pressure, it is also interesting to note that by increasing the pressure within certain limits, I succeeded in greatly enhancing the sensitiveness of the receiver to the action of electric radiation,

In the curves C, D, and E the initial currents were increased with resulting increase of steepness of the curves.

In order to test further the accuracy of the adjustments, I have taken on the same chart, the curve for a constant resistance. In C, the resistance of the receiver at 0·15 volt was found to be 830 ohms. A resistance box having the above resistance was substituted for the receiver, and a curve traced in the usual manner. This curve C′ is seen to be a straight line.

I give below a table showing the results of four sets of experiments on the variation of the resistance r and of conductivity c of the receiver under increasing E. M. F.

Table II.—Showing the Diminution of Resistance of the Receiver, with increasing E. M. F.

E. in volt.	B		C		D		E	
	Current in 1/10⁵ amp.	Resist in ohms.	c	r	c	r	c	r
0·10	9	1,136	12	830	25	400	43	232
0·15	14·2	1,060	18	830	40	375	69	217
0·20	20·5	970	26	770	59	340	102	196
0·25	29·5	850	40	625	83	300	...	...
0·30	40	750	63·5	472	118	254	...	...
0·35	56	620	105	333	...	...	...	...
0·40	85	470	...	...	...	...	...	...

It will be seen that in all the above cases the resistance undergoes a continuous diminution with the increase of E. M. F., and that the diminution of resistance due to electromotive variation is not an abrupt, but essentially a continuous process.

Experiments with Receiver Immersed in Kerosine

In order to find out whether the exclusion of atmospheric action would change the general character of the result, I took observations with a single point iron receiver immersed in kerosine.

Table III.—Showing the Diminution of Resistance with Increasing E. M. F. in a Receiver immersed in Kerosine

E. in volt.	Current in $1/10^6$ amp.	Resistance in ohms.
0·05	15	3,333
0·10	35	2,857
0·15	56	2,678
0·20	78	2,564
0·25	124	2,016
0·30	182	1,648

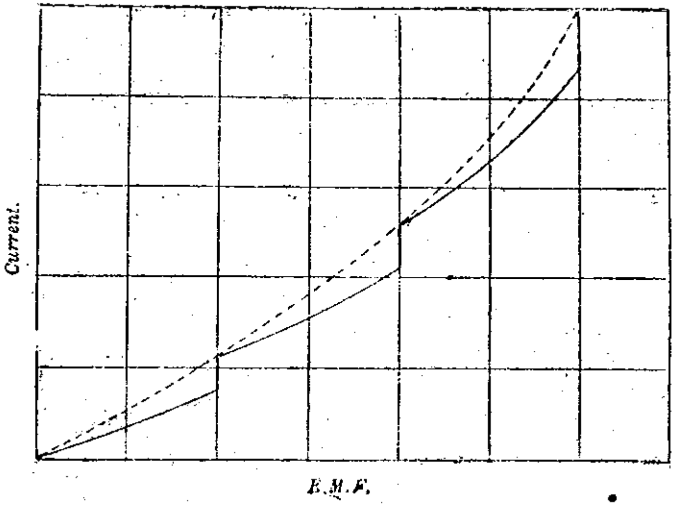

Fig. 53. Effect of Lag.

It will be observed that under the above condition also, there is a continuous diminution of resistance with an increase of E. M. F.

Time-lag

The changes which give rise to the conductivity variation take a short time for their completion. The curves were taken when the electromotive variation was produced at a moderate and uniform speed. But if the electromotive variation is produced quickly and step by step, each step being followed by a pause, then there is an immediate effect, followed by a permanent effect, the galvanometer deflection creeping up to this permanent value. This creeping effect becomes more marked with higher E. M. F. I give above a record where this effect is shown (fig. 53). The vertical

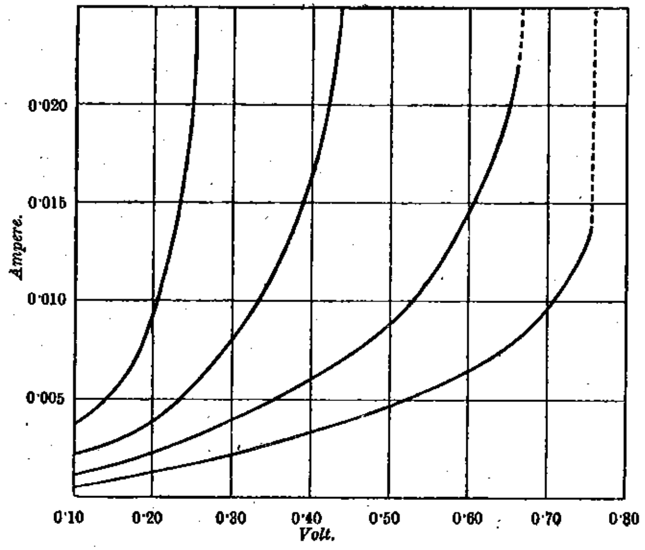

Fig. 54. Curves for Filings.

portions of the curve represent the creeping effect during pause. The conductivity variation thus lags slightly behind the impressed electromotive variation. Certain effects due to this will be noticed later.

Characteristic Curves given by a Mass of Iron Filings

Owing to the multiplicity of contacts the conditions here are not so simple as in the case described above. It will, however, be seen from the curves given in figure 54, that the results are of the same general nature. The resistance undergoes diminution with increasing E. M. F. The curves are steeper with stronger initial currents. Greater intensity of initial current appears also to have the effect of lowering the critical point. I obtained similar results with Mg, and Ni.

It is difficult in one curve to represent adequately the variation of conductivity caused by small, moderate, and excessive increase of E. M. F. Broadly speaking, the curve may be divided into three parts. In the first, when the E. M. F. is low, the change is slight. The curve then becomes very steep in the second part, the conductivity variation being rapid. The increase of conductivity, however, reaches a limit, after which there is little further change. The whole curve is thus somewhat S-shaped.

Conductivity Variation with Cyclic Variation of E. M. F.

When conducting particles of the non-recovering, positive, or iron type are subjected to sudden electric variation due to radiation, a residual effect is observed

indicative of an increase of conductivity or diminution of resistance.

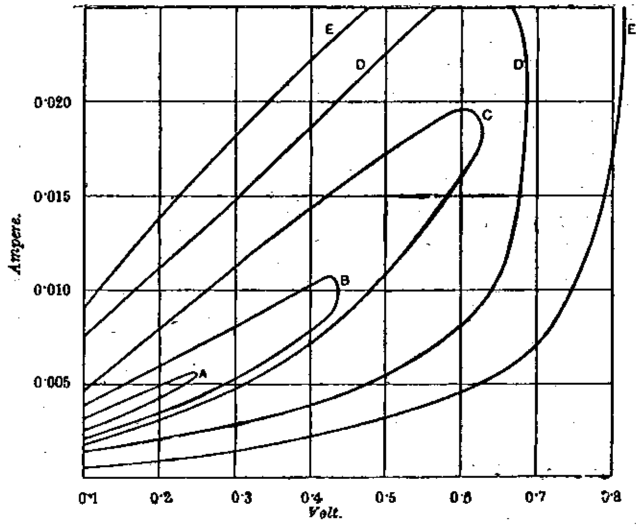

Fig. 55. Cyclic Curves showing Conductivity *Hysteresis*. In each curve the right half is due to increasing, the left half to decreasing E. M. F.

Experiments were next carried out to find whether similar residual effects could be observed when the sensitive substance was carried through a cycle of electromotive variation. I tried both single and multiple contacts.

As stated before, the E. M. F. can be continuously increased by turning the winding wheel which moves the platform uniformly in one direction; the E. M. F. is continuously diminished by turning the wheel in the opposite direction, and thus reversing the motion of the platform. By this means the receiver can be subjected to a cyclic electromotive variation through large or small range at will. I reproduce curves of cyclic variation taken with filings, when the range of electromotive variation is increased from (0·1—0·25 volt) to (0·1—0·81 volt). They will give a good general idea of the phenomena (fig. 55). A series of readings for cyclic variations taken with a single point receiver will be given later.

First, I tried the effect of cyclic variation through a small range, from 0·1 to 0·25 volt. It will be seen that the forward and return curves do not coincide, but enclose a small area. The receiver, in as far as conductivity is a criterion of its physical state, does not regain its original condition. There remains a residual conductivity variation, just as in iron there is a residual magnetism after it has been subjected to a cyclic variation of magnetising force. The residual magnetism disappears on tapping, just as the effect of residual conductivity can be dissipated by the same means.

In curve B, where the range of electromotive variation is still larger, from 0·1 to 0·43 there is a greater divergence between the forward and return curves, and the area enclosed is further increased. An interesting effect, due to *lag*, will be noticed at its far end; though the platform was on its return course, producing a diminution of E. M. F., the current nevertheless continued for a short time to rise. It is thus seen that whatever be the change to which the conductivity variation is due, it lags behind the impressed electromotive variation.

The curves C, D and E, further show that by increasing the range of electromotive variation, the area enclosed between the forward and return curves becomes considerably increased.

I give below detailed readings taken on two occasions with a single point iron receiver, (1) when the range of cyclic variation was small, (2) when the range was comparatively large (*c.f.* Tables IV and V).

Table IV.—Showing the Variation of Current and Resistance with Cyclic Electromotive Variation of Small Range

E. M. F. in volt.	Galvanometer readings. $1\,dn = 1/10^6$ amp.		Resistance in ohms.	
	Direct.	Return.	Direct.	Return.
0·05	10	12	5,000	4,166
0·10	25·5	27	3,920	3,703
0·15	47	49·5 ↑	3,191	3,030 ↑
0·20	↓ 70	75·5	↓ 2,856	2,648
0·25	103	114·5	2,427	2,183
0·30	171	197·5	1,754	1,520

It has been shown that the resistance of the receiver at the higher E. M. F. is less than that at the lower. As the E. M. F. is reduced by the reversed motion of the slider, there is a tendency towards the recovery of the higher resistance which it had at the lower E. M. F. The recovery, however, is not perfect, owing to hysteresis. The recovery is more incomplete if the critical E. M. F. had been exceeded.

There is thus a residual after-effect. In the case given, the initial resistance was 5,000 ohms, and the resistance after cyclic variation through a range of 0·25 volt was 4,166 ohms, or 8/10ths of its original value.

The lag and creeping effects are also noticeable in the forward and return readings.

While the slider moved up to 0·30 volt, the immediate galvanometer reading was 171 divisions, and by the time the slider had commenced its backward movement to the left (producing a diminution of E. M. F.), the current value had risen from 171 to 197·5; the conductivity had gone on increasing, the resistance having fallen from 1,754 to 1,520 ohms.

I now give a table of results for electromotive variation of wider range from 0·1 to 0·6 volt.

Table V.—Showing the Current and Conductivity Variation of a Single-point Iron Receiver, due to Cyclic Electromotive Variation of Comparatively Large Range but Short of Critical Point

E in volt.	G. deflection, 1 $dn = 1/10^6$ amp.		Resistance in ohms.	
	Direct.	Return.	Direct.	Return.
0·05	1·5	13	33,333	3,846
0·20	8	58	25,000	3,448
0·35	34	145	10,294	2,414
0·50	154	346	3,246	1,445
0·60	320		1,875	

In the previous case it was shown that with a cyclic variation of the moderate range of 0·25 volt, the resistance was reduced to 8/10ths; in this case, at double the range, the reduction is very much greater, for the resistance falls to nearly 1/10th of its original value.

This confirms the conclusion previously made that the greater the range of electromotive variation the greater is the reduction of resistance.

Self-Recovering Receiver

It has been shown that receivers which exhibit a diminution of resistance under electric radiation give a characteristic curve which is concave to the axis representing the current, and that in the non-recovering type noticed hitherto, the forward and return curves do not coincide, but enclose an area. I was now interested in finding out what would be the peculiarities of the characteristic curve of receivers showing self-recovery.

I have, as previously mentioned, described a self-recovering receiver of the negative type, made of silver particles. I also succeeded in constructing a self-recovering single point receiver of the positive type, the successive responses of which to brief flashes of radiation are given in figure 56.

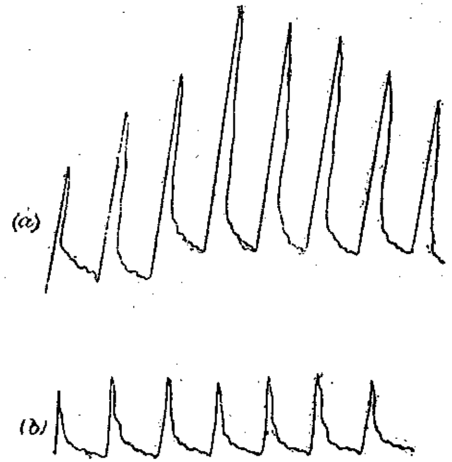

Fig. 56. Response Curves to Single Flashes of Radiation in Self-Recovering Receiver.

In working with receivers which have been at rest for long periods it is often noticed that the response is at first feeble. The sensitiveness soon improves, and may even become excessive; it finally settles down to a moderate and uniform sensitivity. All these phases are well seen in fig. 56 where (*a*) exhibits the preliminary stages, and (*b*) the steadier condition, with more uniform response. The up-curves show the increase of current under the flash of radiation, and the falling and concave portions, the recovery on the cessation of radiation. In self-recovering receivers of the negative type the response curves are the reverse of these, in the sense of the reflected image in a mirror.

The Characteristic Curve of the Self-recovering Receiver of Positive Type

I now subjected the self-recovering receiver to a continuously increasing electromotive variation, and traced the curve. I was not prepared, however, for results so remarkably perfect. In the present case I was not only able to obtain the most important and characteristic effects with great ease and certainty, but also to repeat them, the results of successive experiments being practically identical.

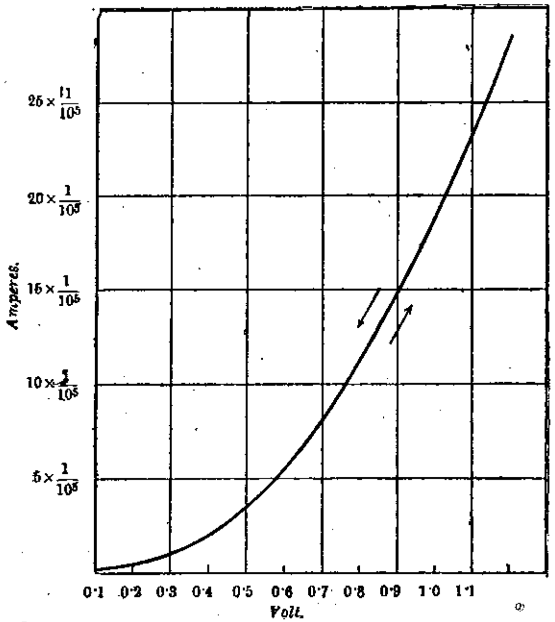

Fig. 57. Characteristic Curve of Self-Recovering Receiver of Positive Type.

The extreme regularity of the observed effect is seen at a glance in figure 57. I give below a table which shows how continuously the resistance is diminished under increasing E. M. F.

Table VI.—Showing Variation of Current and Resistance in Self-recovering Positive Receiver with Increasing E. M. F.

E. M. volt.	Current. 5 $dn = 1/10^5$ amp.	Resistance in ohms.
0·2	2	50,000
0·3	5	30,000
0·4	10	20,000
0·5	17	14,700
0·6	27	11,100
0·7	40	8,750
0·8	55	7,270
0·9	73	6,160
1·0	94	5,320
1·1	115	4,780
1·2	141	4,245

It will be seen that whereas at 0·2 volt the resistance is 50,000 ohms, at 1·2 volt it has undergone an uninterrupted fall to 4,245 ohms, or 1/12th of its original value. There has been no sudden breakdown at any intermediate point.

Figure 58 exhibits the variation of resistance under increasing E. M. F. described in the table VI.

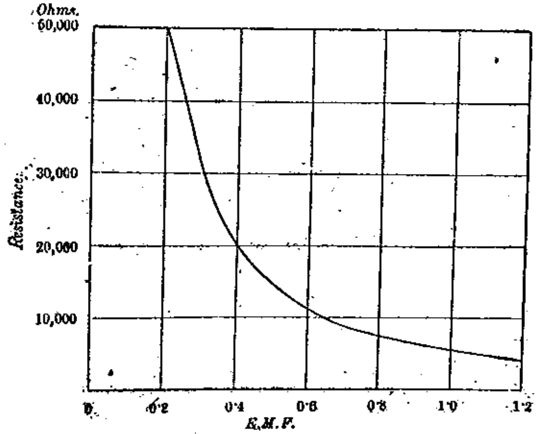

Fig. 58. Curve showing the Variation of Resistance with Increasing E. M. F.

Effect of Cyclic Variation of E. M. F.

But the most astonishing thing about the action of the receiver was that in taking the return curve, I found it practically coinciding *in every part* with the forward curve, so that when the E. M. F. was brought back to its initial value of 0·1 volt, the receiver had completely returned by its original path to its first condition, there being no residual effect. I repeated the experiment many times in succession, but the curves obtained, whether forwards or backwards, were in every case merely superposed on the original. Since the condition of the receiver is exactly the same after many cycles as at the beginning, it is evident that the conductivity variation could not be due essentially to any chemical change, for such changes are irreversible.

The increase of conductivity with increase of E. M. F. is not due to any sudden breakdown, such as fusion between the contact surfaces, for the process described above is anything but abrupt. Again, fusion would have produced a permanent conductivity change, but in the case under review the change is not permanent. Thus, for example, when the applied E. M. F. was 0·2 volt, the current was represented by a deflection of two divisions, the resistance being 50,000 ohms. When the E. M. F. was raised to 0·7 volt, the current increased to 40 divisions, indicating a diminution of resistance which remained at the definite value of 8,750 ohms. If the E. M. F. was again reduced to its original value of 0·2 volt the current was once more two divisions, and the resistance rose to exactly its original value of 50,000 ohms. It would thus appear that—

(1) For a particular E. M. F. there is a definite value of conductivity.

(2) When in a given part of the curve the E. M. F. is increased by a definite amount, the conductivity is also increased in a definite manner. The increased stress produces a definite conductivity distortion, and on the removal of the stress there is a quasi-elastic recovery of its original conductivity.

(3) As the seat of these changes is in the molecular layers at the definite single-point contact, it would appear that the conductivity variation and its recovery are due to molecular distortion and subsequent elastic recovery.

What has been said above of the conductivity change under electromotive variation and the complete recovery is true only when the cycle is completed at a moderate speed, during which, time is allowed for the completion of, or the recovery from, the induced change. But if the cyclic variation be carried out with very great rapidity, the phenomenon of lag comes into play. The conductivity variation then lags behind the impressed electromotive variation, and the receiver does not instantaneously recover its original resistance.

For example, in the case of the self-recovering receiver which at 0·2 volt gave a current represented by two galvanometer divisions, the resistance being equal to 50,000 ohms, the cyclic electromotive variation was quickly carried through the range from 0·2 volt to 1·2 volt and back to 0·2 volt, the immediate value of the current at this last point was not two, but six, divisions of the galvanometer. Thus the receiver, owing to lag, does not instantaneously recover its original resistance; the deflection, however, soon creeps back to two, exhibiting a complete recovery. This characteristic of self-recovery is also exhibited by rapid electromotive variation as under electric radiation (see fig. 56).

Space allows only a brief reference to the characteristic cyclic curve of negative class of substance exemplified by potassium. In this we are presented with the extraordinary phenomenon that an increase of E. M. F. is attended by a diminution of current, so that at a critical E. M. F. the current disappears altogether.

Summary

1. Under the action of electric radiation the conductivity of metallic particles exhibits variation. In the positive class, like iron, there is an increase, and in the negative, like K, a diminution, of conductivity. Each class again falls into two sub-classes, (*a*) sensitive substances which exhibit self-recovery, and (*b*) sensitive substances which do not. In the case of self-recovering substances the conductivity distortion varies with the intensity of radiation. Under the continued action of radiation, the distortion attains a maximum, balanced by a force of restitution, and on the cessation of radiation there is an elastic self-recovery.

2. The three classes of substances, positive, negative and neutral, may be distinguished by their characteristic curves.

3. The change produced in the sensitive substance by the action of radiation is not, normally speaking, chemical.

4. The conductivity change is produced, not only by very rapid, but also by comparatively slow electric variation. Generally speaking, all the conductivity variation effects produced by electric radiation can be reproduced by comparatively slow cyclic electromotive variation.

5. These conductivity changes under cyclic E. M. variation can be continuously recorded by means of the Conductivity Recorder.

6. Electric conduction in metallic particles sensitive to electric radiation does not obey Ohm's law. The conductivity is not constant and independent of the E. M. F., but varies with it. In the positive class the characteristic curve, in which the ordinates represent the currents, and the abscissæ the E. M. F., is concave to the axis of the current. The conductivity increases *continuously* with the increasing E. M. F. The variation of the conductivity in the lower portion of the curve is small, but increases with great rapidity in the upper portion. In the negative class of substance the characteristic curve is convex to the axis of the current.

7. The curve obtained with strong, is steeper than that with feeble, initial current.

8. There is found, especially when the initial current is feeble, a critical E. M. F., at which the conductivity change becomes so rapid as to produce an almost abrupt bend in the curve. Stronger initial current appears not only to lower the critical point, but also to mitigate the abruptness of this change.

9. The effect of E. M. F. in modifying the conductivity of the surface layer is well seen in self-recovering substances. There is a definite conductivity corresponding to a definite E. M. F. As the E. M. F. is increased, the sensitive molecular layer is strained, and a definite increase of conductivity produced. When the increased stress is removed, the corresponding strain also disappears, and there is an elastic recovery to its former molecular and conductive state. Hence, when it is carried through a complete cycle of electromotive variation, with moderate speed, the forward and return curves coincide, and the substance regains, at the end of the cycle, its original molecular condition.

10. This is the case where there is complete recovery on the removal of the stress. With non-recovering substances we find an outstanding residual effect. In a curve taken with cyclic electromotive variation, the forward and return curves do not coincide, but enclose an area. There is a hysteresis. The larger the range of the electromotive variation the greater is the area enclosed. There is a residual conductivity variation, at the end of the cycle, which may be dissipated by mechanical vibration.

(*British Association at Glasgow, Section A, September* 1901.)

XVIII

ON THE SIMILARITY OF EFFECT OF ELECTRICAL STIMULUS ON INORGANIC AND LIVING SUBSTANCES

In working with receivers for electric waves, I found that under continuous stimulation by the oncoming message, the sensitiveness of the metallic detector disappeared. But after a sufficient period of rest it regained once more its normal sensitiveness. In taking records of successive responses, I was surprised to find that they were very similar to those exhibiting fatigue in the animal muscle. And just as animal tissue, after a period of rest, recovers its activity, so did the inorganic receiver recover after an interval of rest.

Thinking that prolonged rest would make the receiver even more sensitive, I laid it aside for several days and was astonished to find that it had become inert. A strong electric shock now stirred it up into readiness for response. Two opposite treatments are thus indicated for fatigue from overwork, and for inertness from long passivity.

A muscle-curve registers the history of the fundamental molecular change produced by excitation in a living tissue, exactly as the curve of molecular reaction registers an analogous change in an inorganic substance. The two represent the same thing; in the latter the molecular upset is evidenced by the change of conductivity, while in the former it is manifested by the change of form. We have thus means of studying molecular reaction produced by stimulus of varying frequency, intensity and duration. An abyss separates the phenomena of living matter from those of inanimate matter. But if we are ever to understand the hidden mechanism of the animal machine it is necessary to face numerous difficulties which at present seem formidable.

I shall now describe the results of comparative study of the curves of molecular reactions of inorganic and living substances. For the former I will take the response of magnetic oxide of iron (Fe_3O_4) to the action of stimulus of electric radiation. Suppose we start with this substance in its normal condition with moderate conductivity, the galvanometer deflection being 50 div., under a definite electromotive force. The deflection of 50 will, therefore, indicate the normal conductivity. Next, under the stimulus of electric waves the induced molecular change causes an increase of conductivity represented by the larger deflection of 100. On the cessation of the stimulus there is a recovery, the galvanometer deflection returning from 100 to the original value 50. The suspended coil of the galvanometer thus moves in response to the varying molecular change induced in the sensitive substance by the action of stimulus. The invisible molecular change is thus revealed by the visible deflection of the galvanometer coil. Curves of molecular change due to electrical stimulation may thus be obtained with galvanometer deflections as ordinates and the periods of stimulation and recovery as abscissæ.

Response to a Single Stimulus

The curve given in fig. 59 represents the effect of instantaneous stimulus on the inorganic receiver. There is a latent period, the response taking place a short time after the incidence of the stimulus; the response continues for a short period even after the cessation of stimulation; it attains a maximum after which the substance begins to recover, at first quickly, then more slowly. In all this, an analogy is found with the response curve of muscles, in which also there is a short phase of latent period, a phase of increasing action and a phase of recovery.

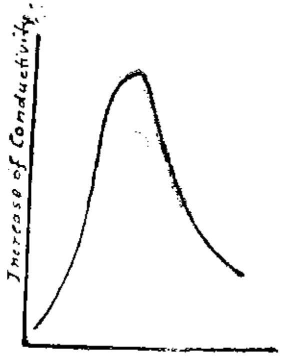

Fig. 59. Curve for Fe_3O_4.

Superposition of Stimuli

Three sets of experiments were carried out (1) on the effect of succession of maximum stimuli; (2) on the summation-effects of medium stimuli with slow intermittence; and (3) on the summation-effects of rapid intermittence.

Maximum stimulation.—By bringing the radiator sufficiently near the inorganic receiver, a maximum effect was observed, the deflection being 230 divisions. Before the substance could recover to any extent, a second stimulus was superposed. This produced no further deflection, but when the second stimulus was applied after recovery, then the second deflection was the same as the first, *i.e.*, 230 divisions.

Medium stimulus, slow intermittence.—In this set of experiments, the radiator was moved further away so that the intensity of the stimulus was moderate; the successive flashes of radiation were applied at intervals of two seconds. These moderate excitations are found to be summated and when in slow succession, the effect of each shock can be distinguished as the steps in the ascending curve, as in fig. 60 (*a*).

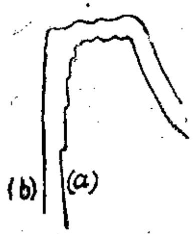

Fig. 60. Superposition of Effects. (*a*) Effect due to Slow Intermittence. (*b*) Tetanic Effect due to High Frequency Intermittence.

Rapid intermittence.—When the stimuli follow each other with great rapidity, the intermittent effects are fused together; the rising curve is found to be unbroken and th ect may be described as 'tetanic' as in fig. 60 (

The respon urves of muscles under the above conditions are lar to the above.

Opposite E cts of Strong and Feeble Stimulus

The respons of many inorganic receivers was found to exhibit the culiarity that while moderate intensity of stimulus produced the normal response of a given sign, a feeble stimulus elicited the opposite reaction, the sign of response being reversed (*cf.* p. 137). I succeeded later in demonstrating the occurrence of similar reactions in living tissues, as for example in the physiological action of drugs, which may be regarded as chemical stimuli. A small 'dose' in such cases is often found to give rise to an effect precisely opposite to that produced by a large dose.

Effect of Variation of Temperature

Variation of temperature produces a marked effect on the response of muscle. At a low temperature the response is very sluggish and the amplitude of response is very much reduced. With rise of temperature the size of response increases and the period of recovery becomes quickened (fig. 61 *a*, *b*). Above a certain optimum the response becomes diminished.

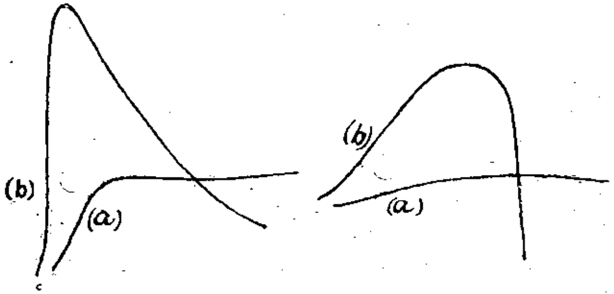

Fig. 61. Effect of Variation of Temperature on Response. Response of Muscle, left; Response of Inorganic receiver, right. (*a*) response at low temperature (*b*) at a higher temperature.

Parallel effects are observed in the response of the inorganic receiver. The curve *a* to the right represents the response of the magnetic oxide of iron receiver when cold; the deflection was moderate and the recovery was extremely slow. On raising the temperature of the receiver to about 15° C. above that of the room, the amplitude of the response was found to be very much increased—nearly threefold.

The recovery became rapid specially in the first part, complete recovery taking place in the course of 75 secs. When the temperature was raised to 100° C., the response became greatly reduced. It is thus seen that a rise of temperature up to an optimum increases the amplitude of response and hastens the recovery in both inorganic and living substances.

Effect of Chemical Substances

Traces of certain substances are found to produce an extraordinarily great increase in the sensibility of the inorganic receivers; these act like stimulants. There are other substances which abolish the sensibility acting like "poisons."

In all the phenomena described above there is no break of continuity. It is difficult to draw a line and say 'here the physical phenomenon ends and the physiological begins' or "that is a phenomenon of dead matter and this a vital phenomenon peculiar to the living"; such lines of demarcation do not exist.

I shall in a future occasion describe a different method namely that of electromotive variation for obtaining the response of inorganic matter, and demonstrate the continuity of response in the living and the non-living.

(*International Congress of Science, Paris* 1900.)

XIX

THE RESPONSE OF INORGANIC MATTER TO MECHANICAL AND ELECTRICAL STIMULUS

Certain changes take place when a living muscle is pinched or an electric shock passed through it. A responsive twitch is produced; the muscle is changed in form, becoming shorter and broader; the particles of the living substance are strained under the stimulus. The effect of the shock then disappears, and the muscle relaxes into its usual form.

This sudden change of form then, is one, but not the only mode of response of a living substance to external stimulus. Under external stimulation the muscle is thrown into a state of strain. On cessation of the stimulus it automatically recovers. As long as it is alive, so long will it respond and recover, being ready again for a new response. This brief disturbance of the living poise, to be immediately restored to equilibrium of itself, is quite unlike the rolling of a stone downhill from a push. For the stone cannot regain its original position; but the living tissue at once reasserts its first stable poise on the cessation of stimulus. Thus a muscle, as long as it is alive, remains ever-responsive. It is in intimate relation with the forces by which it is surrounded, always responding to, and recovering from, the multitudinous stimuli of its physical environment.

The living body is thus affected by external stimuli—mechanical shock, electrical stimulus, and the stimuli of heat and light—which evoke in it corresponding responses.

In the case of the contraction of muscle by mechanical or electric shock, the effect is very quick, and the contraction and relaxation take place in too short a time for detailed observation by ordinary means. Physiologists, therefore, use a contrivance by which the whole process may be recorded automatically. This consists of a lever arrangement, by which the contracting muscle writes down the history of its change, and recovery from that change. The record may be made on a travelling band of paper, which is moving at a uniform rate (fig. 62). A single response to a single stimulus consists of a contractile up-curve followed by the down-curve of recovery, the entire process being completed within a definite period of time. This autographic record gives us the most accurate information as to the characteristic properties and condition of the muscle. It gives us, too, all its individual characteristics.

Just as one wave of sound is distinguished from another by its amplitude, period, and form, so are the curves of different muscles distinguished. For example, the period for tortoise muscle may be as long as several seconds, whereas the period for the wing of an insect is as short as $\frac{1}{300}$th of a second. In the same muscle, again, the form of the curve may undergo changes from fatigue, or from the effects of various drugs. In the autographic record of the progressive death of a muscle, the graph is vigorous at first, but grows lethargic on the approach of death. In some strange way the molecules lose their mobility, rigidity supervenes, and the record of the dying muscle comes to an end. We may thus find out the effects of various external influences by studying the changes in the muscle-curve.

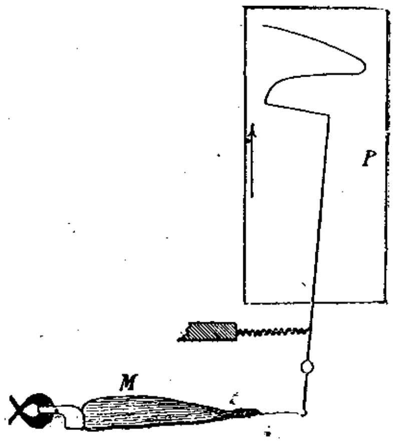

Fig. 62. Mechanical Lever Recorder. The muscle *M* with the attached bone is securely held at one end, the other end being connected with the writing lever. Under the action of stimulus the contracting muscle pulls the lever and moves the tracing point to the right over the travelling recording surface *P*. When the muscle recovers from contraction, the tracing point returns to its original position. See on *P* the record of muscle curve.

We may stimulate the living substance in various ways—by light, or by thermal, chemical, electrical, or mechanical stimuli. Of these, the electric means of stimulation is the most convenient, whereas the mechanical causes fewest complications. With regard to the response of living substances, the most important matters for study are the responses to single stimulus and the modification of response by fatigue and by drugs.

A *single shock* causes a twitch, but the muscle soon recovers its original form. The rising portion of the curve is due to contraction, whereas the falling portion exhibits recovery (see curve in fig. 62).

When the muscle is continuously excited it gets fatigued. The height of the curve becomes continuously less.

Drugs may act as stimulants, or produce depression, according to their nature. As extreme cases of such depressing agents we may instance poisons, which kill the response of living tissue. All signs of irritability then disappear.

Other Modes of Response

This mechanical method of studying the response of living substances is, however, very limited in its application. For example, when a piece of nerve is stimulated, there is no visible change. When light falls on the retina there is no change of form, but it responds by transmitting to the brain a visual impulse. What, then, is this visual impulse which is sent along the optic nerve, causing the sensation of light?

Thanks to the work of Homgren, Dewar, McKendrick and others, it is possible to answer this question. If we excise an eye, say of a frog, and substitute a galvanometer in the visual circuit in the place of the perceiving brain, it is then found that each time a flash of light falls on the eye there is produced an electric response—that is to say, there is a sudden production of a current, which ceases on the cessation of light-stimulus. Stronger light produces stronger electric response in the galvanometer, just as it produces stronger visual sensation in the brain.

The visual circuit is therefore like an electric circuit. The retina is the sensitive element. The nerve is the conductor. The brain like the responding galvanometer is a detector of the impulse. Unless these three elements are in good order, no light-message can be perceived. We must have a sensitive retina, and the conducting nerve, free from injury. Finally, just as the galvanometer will fail to detect a current if it is injured by rough usage, so also after a violent blow, the brain will no longer perceive, though the terminal organ, the retina, and the connecting optic nerve may be intact.

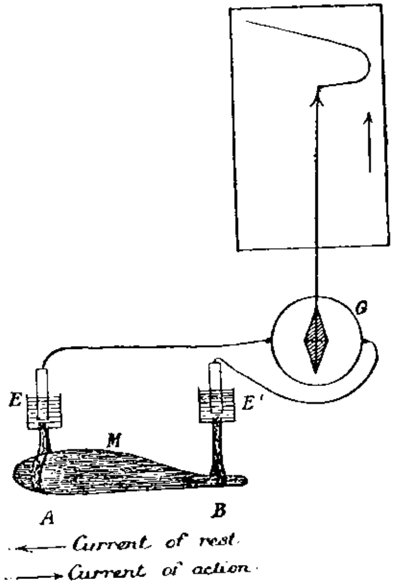

Fig. 63. Magnetic Lever Recorder. *M* muscle; *A* uninjured, *B* injured ends. *E E'* non-polarising electrodes connecting *A* and *B* with galvanometer *G*. Stimulus produces "negative variation" of current of rest. Index connected with galvanometer needle records curve on travelling paper (in practice, moving galvanometer spot of light traces curve on photographic plate). Rising part of curve shows effect of stimulus; descending part, recovery.

Electric Response

If we take a piece of living muscle whose surface is uninjured, then any two points A and B on such a surface being in similar molecular conditions, their electrical level or potential will be the same. They are *iso-electric.* No current will be exhibited by the indicating galvanometer when two non-polarisable electrodes connected with it are applied to A and B. But if one of the two points, say B, be injured by a cut, or burn, then, the conditions of A and B being different, there will be a difference of electric level or potential between them, and a current will flow from the injured to the uninjured, that is from B to A (fig. 63). This current remains approximately constant as long as the muscle is at rest, and is for this reason known as "current of rest." As it is primarily due to injury, it is also known as "current of injury." If now the muscle be thrown into an excitatory state* by stimulus, there will be a greater relative change at the uninjured A, and the original difference of electric level will be disturbed. There is then a *negative* variation or diminution of the original current of rest. This negative variation or "action current" constitutes the "response," the intensity of which increases with the intensity of the stimulus.

If a piece of muscle be taken, and simultaneous records of its response be made by the mechanical and electrical recorders, it will be found that the one is practically a duplicate of the other.

Response in Plants

I find that the electric response seen in animal tissues is also strongly exhibited by the tissues of plants. Various parts of plants—leaves, stems, stalks, and roots—give electric response. In some there is a rapid fatigue, whereas in others there is little fatigue. A more detailed account of these responses and their modifications by anæsthetics, poisons, and other agencies will be found in a subsequent paper.

Universal Applicability of the Test of Electric Response

Nothing has yet been said of the advantage of the electrical over the mechanical method of obtaining response. As has been said before, the mechanical method is limited in its application. A nerve, for example, does not undergo any visible change of form when excited, and its response cannot therefore be detected by this method. But by the electrical method we are able to detect, not only the response of muscles, but also of all forms of living tissue.

The intensity of electrical response is also a measure of physiological activity. When this is diminished by anæsthetics, the electrical responses also become correspondingly diminished. And when the living tissue is in any way killed, the electrical response disappears altogether.

Thus, electrical response is regarded as the criterion between the living and non-living. Where it is, life is said to be; where it is not found, we are in presence of death, or else of that which has never lived: for in this respect there is a great gulf fixed between the organic living and the inorganic or non-living. The phenomena of the inorganic are supposed to be dominated merely by physical forces, while on the other side of the chasm, in the domain of the living, inscrutable vital phenomena, of which electric response is the sign-manual, suddenly come into action.

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* The excitatory reaction is, in the case of some living substances, of a more or less local character. In others, as nerves, it may be conducted to distant points.

But is it true that the inorganic are irresponsive, that forces evoke in them no answering thrill? Are their particles for ever locked in the rigid grasp of immobility? As regards response, is the chasm between the living and inorganic really impassable?

Inorganic Response

Let us take a piece of thin wire from which all strains have been removed and hold it clamped in the middle at C (fig. 64).

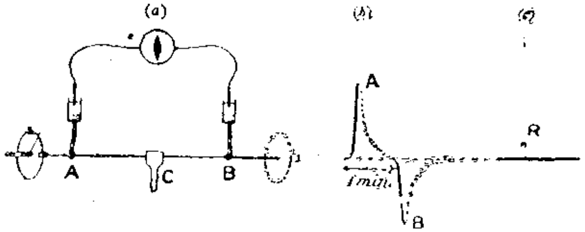

Fig. 64. Electric Response in Metals. (*a*) Method of block; (*b*) Equal and opposite responses when the ends A and B are stimulated; the dotted portions of the curve show recovery; (c) Balancing effect when both the ends are stimulated simultaneously.

A and B will be found *iso-electric* and no current will pass through the galvanometer. If we now stimulate the end A by a tap, or better still by rapid torsional vibration, a " current of action " will be found to flow in the wire in one direction. Stimulation of B on the other hand, gives rise to a current in the opposite direction. The object of the block C is to prevent the molecular disturbance produced by stimulus at one end of the wire from reaching the other.

Quantitative stimulation is applied by producing a sudden torsional vibration, say of 90°, to the end A, with the result of an up-response of the galvanometer; on application of similar stimulus to the end B, there

is produced an equal and opposite response (fig. 64). If now both the ends A and B are stimulated simultaneously, the responsive electromotive variation at the two ends will continuously balance each other and the galvanometer spot will remain stationary. Fig. 65 gives the record of series of equal and opposite responses by alternate stimulation of A and B.

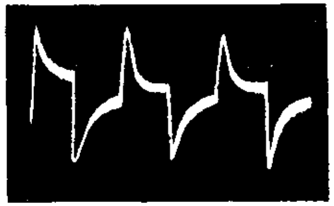

Fig. 65. Photographic Record of Equal and opposite Responses exhibited by stimulations of A and B (Tin).

The similarities of response of inorganic and living substances are now sufficiently evident. We have to extend the inquiry to see whether this similarity extends to this point only, or goes still further. Are the response-curves of the inorganic modified by the influence of external agencies, as the living responses are found to be?

Effect of Superposition of Stimuli

It has been said that under rapidly succeeding stimuli, the intermittent effects of single shocks become fused, and the muscle responds by an almost unbroken tetanic curve (fig. 66). If the frequency is not sufficiently great, there is an incomplete tetanus and the response-curve becomes jagged.

The very same thing occurs in metals. I subject the wire to quickly succeeding vibrations. The curve rises to its maximum; further stimulation adds nothing to the effect, and the deflection is held, as it were rigid,

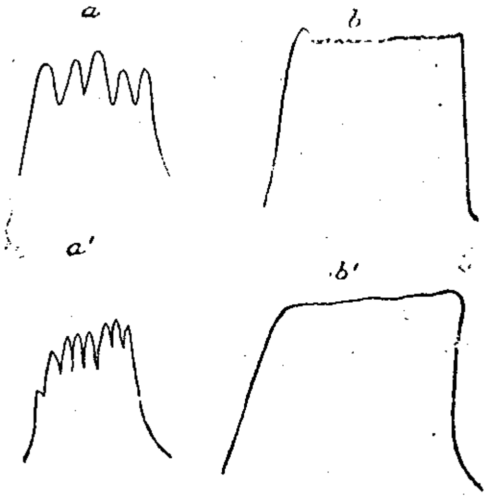

Fig. 66. Effects analogous to (*a*) incomplete and (*b*) complete tetanus in tin. (*a′*) Incomplete and (*b′*) complete tetanus in muscle.

so long as the stimulation is kept up. With lesser frequency of stimulation the tetanus is incomplete, and the curve becomes jagged (fig. 66).

Fatigue

Amongst living substances the nerve is practically indefatigable. Successive curves are exactly similar. Muscles, however, exhibit fatigue, which disappears after a period of rest.

Inorganic substances likewise exhibit fatigue specially after prolonged action. The fatigue curve here reproduced was obtained from tin that had been subjected to very prolonged stimulation; its remarkable similarity to the curve of fatigue in muscles will be at once

apparent (fig. 67). Fatigue in metal is also removed by a period of rest.

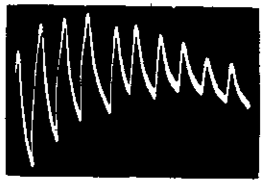

Fig. 67. Photographic record of fatigue in tin.

Stimulus of Light

I have in this investigation mainly used the mechanical form of stimulation as being the simplest and giving rise to fewest complications. Time does not allow of my entering here upon the subject of the response under electric stimulation. I may, however, say a few words on the effect of the stimulus of light.

If one of the sensitised wires in the cell already described be subjected to light it gives an electric response, and under certain circumstances an oscillatory after-effect is seen to occur on the cessation of light. This latter fact probably explains certain phenomena of visual recurrence to be noticed presently.

Artificial Retina

The molecular strain produced by stimulus can not only be detected by the phenomena of electromotive variation, but also by conductivity variation. Acting on this principle, I have been able to construct an artificial retina constructed of galena. The sensitive receiver is placed inside a hollow spherical case, provided with a circular opening in front, in which a glass lens is placed, corresponding to the crystalline lens. You now see before you a complete model of an artificial eye. When this is interposed in an electric circuit, with a sensitive galvanometer as indicator, you observe the response to a flash of light by the galvanometer deflection. I throw red, yellow, green and violet lights upon it in succession, to all of which it responds. Note how strong is the action of yellow light, the response to violet being relatively feeble. Indeed, the most striking peculiarity of this eye is that it can see lights not only some way beyond the violet, but also in regions far below the infra-red, in the invisible regions of electric radiation. It is in fact a *Tejometer* (Sanskrit *tej*-radiation), or universal radiometer.

Observe how each flash of invisible light I am producing with this electric radiation apparatus, calls forth an immediate response, and how the eye automatically recovers without external aid. This will show the possibility of an automatic receiver which will record Hertzian wave-messages without the intervention of the crude tapping device.

This retina has, as will be seen with regard to spectral vision, an enormous range, extending far beyond the visual limits. We can, however, reduce its powers to a merely human level by furnishing it with a water lens, which, in its liquid constitution, approximates closer to the lens of the eye than does the glass substitute. In this case the invisible radiations are absorbed by the liquid, and do not reach the sensitive retina. Perhaps we do not sufficiently appreciate, especially in these days of space-signalling by Hertzian waves, the importance of that protective contrivance which veils our sense against insufferable radiance.

Binocular Alternation of Vision

I have referred to the fact that sometimes on the cessation of light, an after-oscillation is observed, which may correspond to the after-oscillations of the retina, and give a probable explanation of the phenomena of recurrent vision. When we have looked at a bright object for some time with one eye, we find, on closing both eyes, that the image alternately appears and disappears. It was while studying this subject that I came upon the curious fact that the two eyes do not see equally well at a given instant, but take up, as it were, the work of seeing, and then resting, alternately. There is thus a relative retardation of half a period as regards maximum sensation in the two retinas. This may be demonstrated by means of a stereoscope, carrying, instead of stereo-photographs, incised plates through which we look at light. The design consists of two slanting cuts at a suitable distance from each other. One cut, R, slants to the right, and the other, L, to the left (see fig. 68). When the design is looked at through the stereoscope, the right eye will see, say R, and the left L; the two images will appear superimposed, and we see an inclined cross. When the stereoscope is turned towards the sky, and the cross looked at steadily for some time, it will be found, owing to the alternation already referred to, that while one arm of the cross begins to be dim, the other becomes bright and *vice versa.* The alternate fluctuations become far more conspicuous when the eyes are closed; the pure oscillatory after-effects of the strained sensitive molecules in the retina are then obtained in a most vivid manner. After looking through the stereoscope for ten seconds or more, the eyes are closed. The first effect observed is one of darkness, due to the rebound. Then *one* luminous arm of the cross first projects aslant the dark field, and then slowly disappears; after which the second (perceived by the other eye) shoots out suddenly in a direction athwart the first. This alternation proceeds for a long time, and produces the curious effect of two luminous blades crossing and re-crossing each other. Another method of bringing out the same facts in a still more striking manner, is to look at two different sets of writing, with the two eyes. The resultant effect is a blurr, due to superposition, and the inscription cannot be read with the eyes open. But on closing them, the composite image is analysed into its component parts, and thus we are enabled to read better with eyes shut than open!

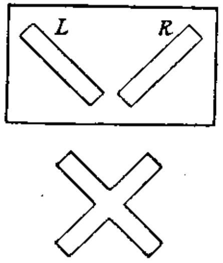

Fig. 68. Stereoscopic design to show binocular alternation of vision.

It will thus be seen how, from observing the peculiarities of an artificial organ, we are led to discover unsuspected peculiarities in our own. We stand here on the threshold of a very extended inquiry, of which I can only say that as it has been possible to construct an artificial retina, so I believe it may not be impossible to imitate also other organs of sense.

Effects of Chemical Reagents

I now return to the consideration of mechanical stimulus and the modification of its responses, as shown by metals. We have seen the remarkable parallelism between organic and inorganic responses under various conditions. There still remains the study of the effects of chemical reagents. Drugs profoundly modify the response of living substances; the effects of which may be classified under three classes, some acting as stimulants, others as depressors, and yet others again as poisons, by which response is permanently abolished. Amongst the last may be mentioned mercuric chloride, oxalic acid and others. Again, drugs which in large doses become poisons, may, when applied in small quantities, act as stimulants.

It may be thought that to these phenomena, inorganic matter could offer no parallel. For they involve possibilities which have been regarded as exclusively physiological. Accustomed in the animal to find the responsive condition transformed into the irresponsive state at the moment of death, we look on this sequence as peculiar to the world of the living. And on this fact is based the supreme test by which physical and physiological phenomena are differentiated. That only can be called living which is capable of dying, we say, and death can be accelerated by the administration of poison. The sign of life as given by the electric pulses then wanes, till it ceases altogether. Molecular immobility—the rigor of death—supervenes, and that which was living is no longer alive.

Is it credible that we might, in like manner, kill inorganic response by the administration of poison? Could we by this means induce a condition of immobility in metals, so that, under its influence, their electric responses should wane and die out altogether?

Before we attempt the action of poisons let us study the exciting effect of stimulants. You observe the normal extent of response under successive uniform stimuli applied to one wire of the cell. I now add a few drops of diluted solution of sodium carbonate and you observe the growing exaltation of the response. (fig. 69).

I now pass on to the effect of poisons. Any of the substances already enumerated may be used as the toxic agent. After obtaining the normal response I apply a poisonous solution of oxalic acid. The electric response is now completely killed and all our efforts, by intense stimulation to reawaken them, fail (fig. 70).

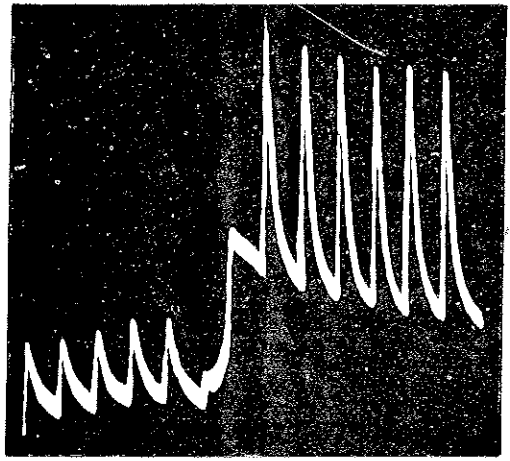

Fig. 69. Stimulating action of Na_2CO_3 on tin.

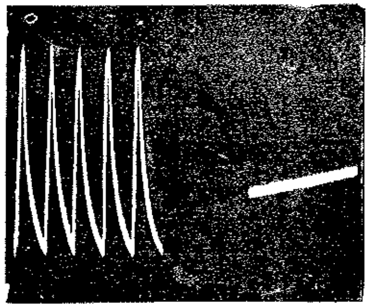

Fig. 70. Abolition of Response by Oxalic acid.

But we may, sometimes at least, by the timely application of a suitable antidote, revive the dying response, as I do now. See how the lethargy of immobility passes away; the electric throb grows stronger and stronger, and the response in the piece of metal becomes normal once more.

There remains the very curious phenomenon, known not only to students of physiological response but also in medical practice, that of the opposite effects produced by the same drug when given in large or in small doses. Here too we have the same phenomenon reproduced in an extraordinary manner in inorganic response. The same agent which becomes a poison in large quantities thus acts as a stimulant when applied in small doses.

I have shown you this evening autographic records of responses of the living and non-living. How similar are the writings! So similar indeed that you cannot tell one from the other apart. We have watched the responsive pulses wax and wane in the one as in the other. We have seen response sinking under fatigue, becoming exalted under stimulants, and being "killed" by poisons, in the non-living as in the living.

Amongst such phenomena, how can we draw a line of demarcation, and say, "here the physical process ends, and there the physiological begins"? No such barriers exist.

Do not the two sets of records tell us of some property of matter common and persistent? Do they not show us that the responsive processes, seen in life, have been foreshadowed in non-life?—that the physiological is, after all, but an expression of the physico-chemical, and that there is no abrupt break, but a continuity?

If it be so, we shall turn with renewed courage to the investigation of mysteries which have long eluded us. For every step of science has been made by the inclusion of what seemed contradictory or capricious in a new and harmonious simplicity. Her advances have been always towards a clearer perception of underlying unity in apparent diversity.

(*Friday Evening Discourse, Royal Institution, May* 1901)

XX

ON ELECTROMOTIVE WAVE ACCOMPANYING MECHANICAL DISTURBANCE IN METALS IN CONTACT WITH ELECTROLYTE

Take a rod of metal, and connect the two points A and B with a galvanometer by means of non-polarisable electrodes. (Fig. 71*a.*) If the point O is struck, a wave of molecular disturbance will reach A and B. It will be shown that this is attended by a wave of electric variation. The mechanical and the attendant electrical disturbance will reach a maximum and then gradually subside. The resultant effect on the galvanometer will be due to $E_A - E_B$ where E_A and E_B are

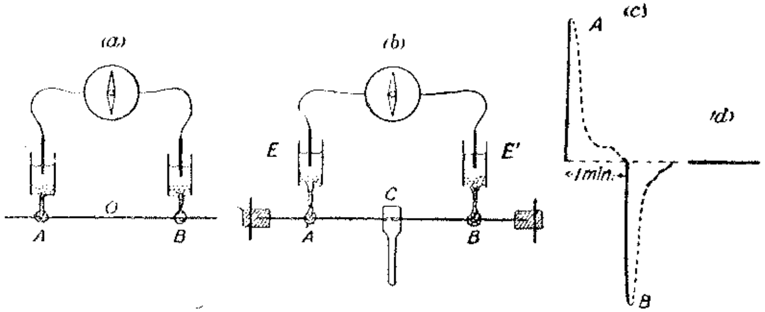

Fig. 71. In (*a*) mechanical disturbance at O produces similar electrical variations at A and B ; there is no resultant effect. In (*b*) owing to a clamp, molecular disturbance initiated at A cannot reach B. A tap or vibration imparted to the end A produces responsive current which flows in the wire from the unexcited B to the excited end A. Disturbance at B gives rise to a current in the opposite direction. (*c*) gives the record of the response to equal stimuli applied to A and B. The ascending part of the curve shows the effect of stimulus, the falling part shows recovery. (*d*) Simultaneous stimulation of A and B gives no resultant response. (In the records dotted lines represent recovery.)

the electric variations induced at A and B. The electric changes at A and B will continuously balance each other, and the resultant effect on the galvanometer will be zero, when the mechanical disturbance reaches A and B at the same time and with the same intensity, when the molecular condition is similar at the two points, and when the rate of rise and subsidence of disturbance is the same at the two points. In order that a resultant response may be exhibited, matters have to be so arranged that (1) the disturbance reaches one point, say A and not B, and *vice versâ*. This may be accomplished by the method of block. Again, a resultant differential action may be obtained even when the disturbance reaches both A and B, if the electrical excitability of one point is relatively exalted or depressed by physical or chemical means. Besides the method of the block there are thus two other means of obtaining a resultant response, (2) by the method of relative exaltation, (3) by the method of relative depression.

Method of Block

The electromotive effect described below can be obtained with all metals. A piece of " tin " wire (an alloy of tin and lead used as electric fuse) will be found to give very good results. A specimen of wire 1 mm. in diameter, 10 cm. in length, is mounted in the apparatus. Two strips of cloth moistened with water or dilute salt solution are securely tied round two points A and B. Electric connections are made with the indicating galvanometer by means of non-polarisable electrodes (Zn in ZnSO solution). Special precautions are taken so that there is no variation of contact. If a sharp tap be now given near A, a transitory electrical current in response to the disturbance will be found to flow round the circuit, in a definite direction. Disturbance of B gives rise to a current in the reverse direction. For quantitative measurement it is necessary to have the intensity of stimulus maintained uniform, or increased or decreased in a definite manner. Instead of a tap, the stimulus of torsional vibration is more satisfactory. By maintaining the amplitude of vibration constant, or increasing or decreasing the amplitude, we can either keep the stimulus constant, or increase or decrease it in a quantitative manner. I shall first describe some of the typical results which may be obtained with the simple " straight wire form " of the apparatus. Worked with care it gives consistent and good results. For quantitative measurements requiring the greatest exactitude the " cell form," to be presently described, will be found more satisfactory.

Recording Apparatus.—The galvanometer used is a sensitive dead-beat D'Arsonval. The records are taken by means of a cylindrical modification of the response recorder described in a previous paper, or by means of photography. In the latter method, a clockwork moves the photographic plate at a uniform rate and a curve is traced on the plate by the moving galvanometer spot of light. The disturbance of molecular equilibrium caused by the stimulus is attended by an electromotive variation, which gradually disappears on the restoration of molecular equilibrium. The rising portion of the response curve shows the electromotive effect, due to stimulus, and the falling portion the recovery. The ordinate represents the electromotive variation, and the abscissa the time.

Experiments for Exhibition of Balancing Effect

If the wire had been carefully annealed, the molecular conditions of its different points are approximately the same. The wire will therefore be practically iso-electric throughout its length. If the wire be now held near the middle by the clamp, and a vibration through an amplitude of, say, 90° be given to the end A, an upward deflection will be produced; an equal and opposite deflection will be produced by similar vibration of B (fig. 71, *c*). If both the ends are simultaneously vibrated, the electromotive variation at the two ends will continuously balance each other, and the galvanometer spot will remain quiescent (fig. 71, *d*). The clamp is next removed, and the wire vibrated as a whole; the stimulation of A and B being the same, there is no resultant deflection. Having found the balancing point for the clamp (which is at or near the middle), if the clamp be now shifted to the left, on simultaneous vibration of A and B, the A effect will relatively be the stronger (inasmuch as the torsional vibration of A is increased and that of B decreased), and there is produced a resultant upward deflection. Thus keeping the rest of the circuit untouched, by merely moving the clamp from the left, past the balancing position to the right we get either a positive or zero or a negative resultant effect. This can be repeated any number of times. The experiment shows further that when the amplitude of vibration is kept constant, the intensity of electromotive effect is increased by shortening the wire. The normal direction of the current of response in the wire is in the majority of metals, from the relatively less to the relatively more excited point.

The form of the response curve, stimulus remaining constant, is modified by the molecular condition of the wire. A wire in a sluggish condition shows feeble response, the recovery being also slow. The same wire after it has been vibrated for a time exhibits a stronger response. Longer time is required for recovery from the action of a stronger stimulus.

Comparison of Electric Excitability of Two Points by the Method of Balance

As already stated, when the clamp is put at the balancing position, alternate equal stimulations of A and B produce equal and opposite electromotive responses, and when the two ends are stimulated simultaneously there is no resultant effect.

Increased Excitability produced by Preliminary Vibration.—If now one-half of the wire, say the A half, be vibrated for a time, the electric excitability of that half will be found to be more or less permanently augmented, presumably by increased molecular mobility conferred by vibration. The response of A would now be found to be greatly enhanced, as compared with its previous response, the response of B remaining the same as before. If now both the ends are simultaneously vibrated, the previous balance will be found to be upset, the resultant showing that A in consequence of previous stimulation, has been rendered the more excitable.

If B be now vibrated for a time, the former approximate balance will be re-established by the enhanced responsiveness of B. Thus the following results are obtained with the clamp at the approximate balancing point :

	Response of A.	Response of B.	Resultant response.
	Divisions.	Divisions.	Divisions.
Approximate balance .	+5	—4·5	+0·5
After the end A has been vibrated.	+10·5	—4·5	+6·0
After the end B has been vibrated for an equal length of time.	+10·5	—9·5	+1·0

Effect of Chemical Reagents.—It will be shown that keeping the electrolyte by which contact is made constant, the electric excitability of the wire depends on the molecular condition of the wire. Certain electrolytes, such as dilute solution of NaCl, dilute solution of bichromate of potash and others, are normal in their action, that is to say, with such contacts the response to stimulation is practically the same as with distilled water contact.

Contact made with dilute NaCl solution may therefore be regarded as the normal contact. There are again certain chemical reagents which enhance the electrical excitability ; others on the contrary produce great depression, or abolition of excitability.

Electric Comparator

We may compare the relative electric excitability conferred by chemical reagents by the method of balance. Having previously obtained a balance (with water or dilute NaCl solution at A and B), one contact, say A, is touched with a few drops of very dilute Na_2CO_3, which is an exciting agent. The electric excitability of A will now be found to be greater than that of B as demonstrated by the upsetting of the previous balance, the resultant current being now towards the more excitable A.

	Response of A.	Response of B.	Resultant response.
Both contacts of normal saline.	+12	—12	0
Contact A touched with Na_2CO_3 solution.	+32	—12	+20

Similarly, when A is depressed by a trace of oxalic acid, the electric excitability of A is less than that of B, the resultant deflection being now downwards (current of response towards the relatively more responsive B). It is to be remembered that in all cases *the resultant current of response in the wire is towards the more excitable point.*

An interesting line of investigation rendered possible by a modification of method of balance described above is to compare the relative excitability induced by various chemical reagents, the influence of different strengths of the same reagent, and the modification of the effect by the duration of application. We may thus compare the effect of the reagent in relation to the normal effect of water or dilute NaCl solution. There is again an extremely delicate method of comparison of the relative effects of a series of compounds like Na_2CO_3, K_2CO_3, etc. Balance having been previously obtained between the normal sensitiveness of A and B, the two different solutions are now applied at the two points; the slightest difference in their relative action is at once exhibited by the upsetting of the balance during stimulation, the direction of the resultant deflection indicating the more stimulating reagent.

Resultant Response by Method of Relative Depression or Exaltation

From what has been said, it will be seen that by rendering A and B unequally excitable, a resultant response may be obtained. The block may be abolished, and the wire may be vibrated as a whole; the response will now be due to the differential effect at A and B. For producing difference in excitability we may subject one point, say A, to a preliminary vibration, or apply at the point a suitable chemical reagent. By the application of the latter there will be a small P. D. between A and B, which will simply produce a displacement of the zero. (By means of a potentiometer the galvanometer spot may be brought back to the original position). The displacement of the zero does not affect the general result. The direction of this more or less permanent current, due to the small P. D., gives no indication of the direction of current of response; the direction of the latter is determined by the rule that the responsive current flows towards the more excitable point. The electromotive response induced by mechanical stimulation is algebraically superposed on the existing P. D. The deflection takes place from the modified zero, to which the spot returns during recovery. I give four records (fig. 72): in (*a*) A is touched with Na_2CO_3 (which is an excitant): a permanent current flows from B to A: response to stimulus is in the same direction as the permanent current (positive variation); in (*b*) A is touched with a trace of oxalic acid (which depresses the excitability), the permanent current is in the same direction as before, but the current of response is in the opposite direction (negative variation); in (*c*) A is touched with dilute KHO (3 parts in 1000), the response is exhibited by a positive variation; in (*d*) A is touched with stronger KHO (3 parts in 100), the response is now exhibited by a negative variation. The last two apparently anomalous results are due to the fact (which will be demonstrated later) that KHO in minute quantities is an excitant, while in larger quantities it is a depressant.

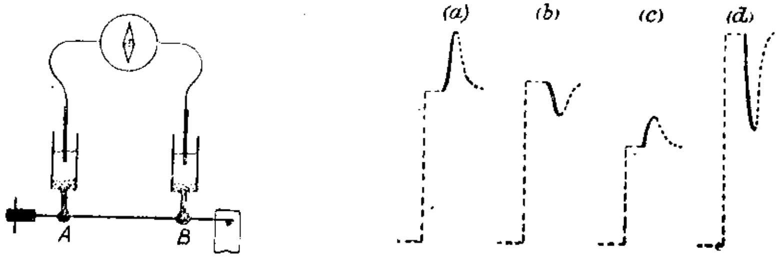

Fig. 72. Response by Method of Relative Depression or Exaltation.

(*a*) Response when A is treated with sodium carbonate—an apparent positive variation.
(*b*) ,, ,, ,, ,, oxalic acid—an apparent negative variation.
(*c*) ,, ,, ,, ,, very dilute potash—positive variation.
(*d*) ,, ,, ,, ,, strong potash—negative variation.

This response is up when A is more excitable and down when B is more excitable.

Lines thus — — — indicate direction of permanent current.

	Permanent current.	Current of response.
A treated with sodium carbonate .	←	←
,, ,, oxalic acid . . .	←	→
,, ,, very dilute potash .	←	←
,, ,, strong potash . .	←	→

Current of response is always towards the more excitable point.

Detection of Minute Physico-chemical Change

I will now describe an experiment which will show in a striking manner how exceedingly delicate is the method of electric response to stimulation, and how by its means we can detect and measure traces of physico-chemical changes in different parts of the same solid. Take a wire and touch two points, one with Na_2CO_3 solution the other with oxalic acid. Wash the wire. There is no trace left of the previous treatment. Let one contact be permanently made at a normal or previously unacted point N. Let the other exploring contact be moved along from the other end towards N, the wire being mechanically stimulated during the test. The galvanometer spot remains quiescent as long as the exploring contact is over normal areas. But as soon as it touches the zone on which is impressed the invisible image of physico-chemical change, the differential effect of stimulus at once reveals it by producing a vigorous movement of the galvanometer spot. At N_1 there was no movement, but there was an upward movement of response when the explorer came over the stimulated area " Carbonate." As the explorer passed on to N_2 there was a cessation of movement, but when it reached the depressed area marked " Oxalic " there was a vigorous movement downwards (fig. 73).

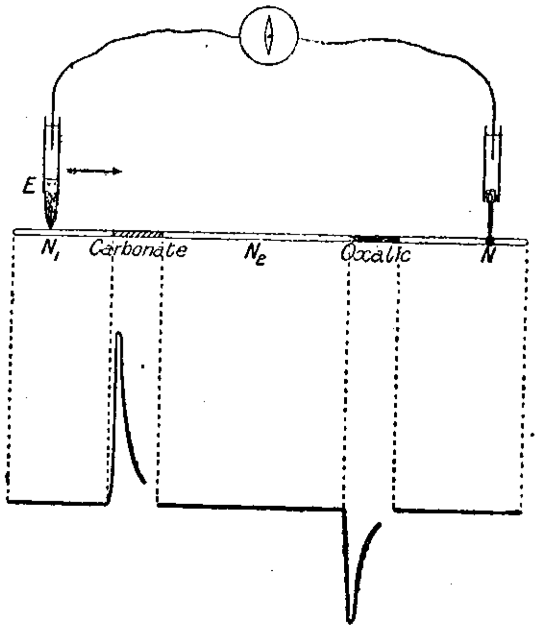

Fig. 73. Electro-molecular Explorer.

Interference Effects

I have already described a case of interference in the galvanometric effect when the two points A and B in similar molecular conditions are simultaneously acted on by the same mechanical stimulus. Under these conditions the electric variation at the two points *continuously* balance each other, and there is no resultant effect.

When one point is acted on by a chemical reagent, not only is its electric excitability changed, but its time relations—its latent period, the time-rate of its acquiring the maximum electric variation, and the recovery from the effect of stimulus—become also modified. Using the block method, we may place a drop of excitant Na_2CO_3 on A and depressant KBr on B. On simultaneous vibration of A and B, the A effect being relatively much stronger than B effect, the resultant is an upward deflection. But on moving the balancing clamp away from A (thus decreasing the stimulation intensity of A and increasing that of B) we can find a point where the A effect is equal and opposite to the B effect. But owing to change of time relations, simultaneous vibration of A and B no longer gives a continuous balance; we obtain instead a diphasic variation. The diphasic curve thus obtained is exactly the same as the resultant curve deduced from the algebraic summation of the A and B curves obtained separately.

Continuous Transformation from Positive to Negative through an Intermediate Diphasic Response.—In the following record, fig. 74, I succeeded in obtaining a continuous transformation from positive to negative due to induced changes in the relative sensitiveness of the two contacts. I found that traces of after-effect due to application of Na_2CO_3, even after it is washed off, remain for a time, the increased sensitiveness conferred disappearing gradually. Again, if we apply Na_2CO_3 solution to a fresh point, the sensitiveness *gradually* increases. There is another interesting point, *viz.*, that the beginning of response is earlier when the application of Na_2CO_3 is fresh. In the experiment whose record is given, the wire is held at one end, and successive uniform vibrations imparted to the wire as a whole at intervals of one minute by means of a torsion head at the other end. Owing to after-effect of previous applications of Na_2CO_3, the sensitiveness of A is at the beginning great, hence the resultant response at the commencement is positive or upward. Dilute solution of Na_2CO_3 is next applied to B. The response of B (down) begins earlier, and continues to grow stronger and stronger. The response therefore shows a preliminary negative twitch of B followed by positive variation of A. The negative grows continuously. At the fifth response, the two components, negative and positive, of the double response become equal; after that, the negative becomes very prominent, the positive dwindling into a feeble and inconspicuous response.

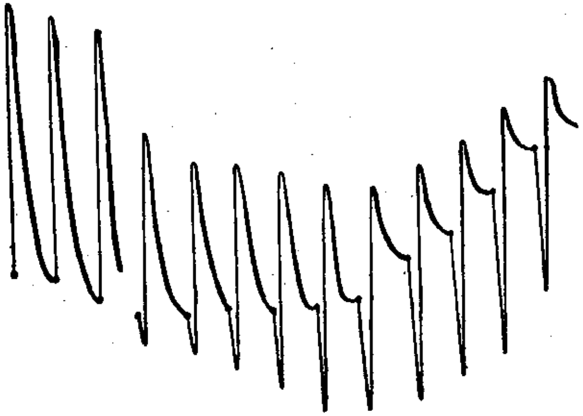

Fig. 74. Transformation from positive to negative through intermediate diphasic variation. Thick dots represent times of application of stimulus.

Modification of the Apparatus into " Cell Form "

The series in fig. 75 explains the transformation from the " straight wire " to " cell " form. The wires A and B, cut from the same piece, are clamped separately below; vibration of A (the amplitude of which is measured by a graduated circle) gives rise to a responsive current in one direction; vibration of B produces a current in the opposite direction. Every experiment can thus be verified by corroborative and reversal effects. The intensity of electromotive response varies with the substance, and is sometimes considerable, for example, with " tin," a single vibration may give rise to as high a value as 0·4 volt. The intensity of response does not depend on the chemical activity of the substance, for the electromotive variation in the relatively inactive tin is greater than that in zinc. Again, the sign of response, positive or negative, is sometimes modified by the molecular condition of the wire (see below). In the cell form of apparatus the wires are immersed to a definite depth in the electrolyte; there is thus a perfect and invariable contact between the wire and the electrolyte. The wire is clamped below, and torsional vibration gives rise to a strong electrical response. If the wire be carefully unclamped, vibration is found to cause no electrical response. As all the rest of the circuit is kept absolutely the same in the two different sets of experiments, the results offer conclusive proof that the responsive electromotive variation is solely due to the mechanical stimulation of the acted wire. The excitatory effect due to stimulation persists for a time. This is demonstrated by keeping the galvanometer circuit open during the application of stimulus, and completing it at various short intervals

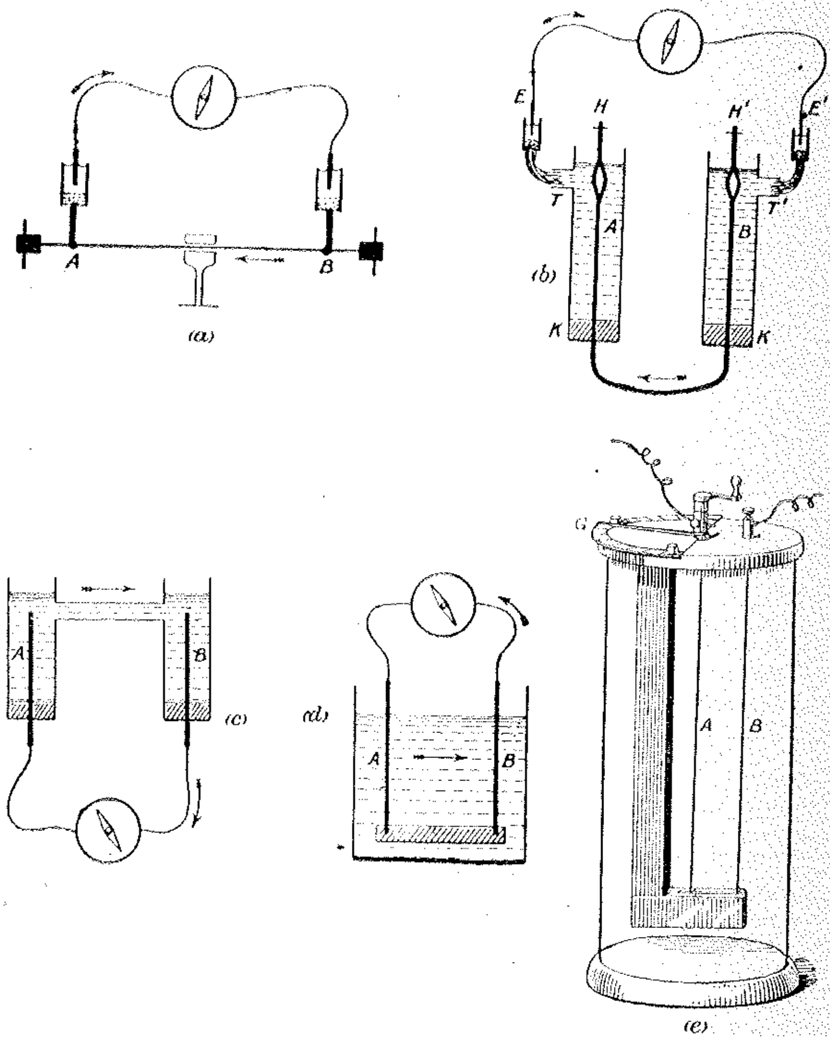

Fig. 75. Successive modifications of the " straight wire " ending in " cell form." (*b*) shows how the ends of A and B of the wire may be vibrated by ebonite clip-holders, H and H'. When A is excited, current of response *in the wire*, normally speaking, is from the unexcited B to the excited A. The stimulated wire becomes zincoid. Note that though the current of response is constant in direction, the galvanometer deflection in (*d*) will be opposite in direction to (*b*). In (*e*) is shown one of the two graduated circles by which the amplitude of vibration is measured.

after its cessation, when a persisting electrical effect diminishing rapidly with time will be observed. When the wire is brought to the normal condition, successive responses to uniform stimuli are exactly similar in the case of metals which, like tin, show no fatigue. I usually interpose a high external resistance, varying from 1 to 5 megohms, so that the galvanometer deflections are proportional to the electromotive variations; the internal resistance of the cell and the variation of that resistance by the addition of chemical reagents are thus rendered quite negligible. Ordinarily tap-water is used as the electrolyte. The responses obtained with tap-water are practically the same as those obtained with distilled water. Zinc wires in $ZnSO_4$ solution give responses similar in character to those given by, for example, Pt or Sn in water.

Character and Intensity of Response dependent on Molecular Condition

The following experiments show how the phenomenon of response is intimately connected with the molecular condition of the acted wire:—

Effect of Annealing.—The photographic records, given in fig. 76, show the equal and opposite responses in A and B wires to a succession of uniform stimuli. Hot water was now substituted for the cold water (too high a temperature temporarily reduces the response); the cell was then allowed to cool to its old temperature. Records show how the process of annealing had greatly enhanced the amplitude of response.

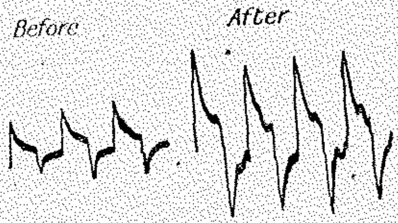

Fig. 76. Series of responses, to uniform stimuli, of both A and B wires, before and after annealing.

Effect of Previous Vibration.—The increased sensitiveness conferred by previous vibration has already been referred to before. I give below a record (fig. 77) obtained with platinum; this and similar results obtained with other metals clearly show the enhancement of response after preliminary stimulation.

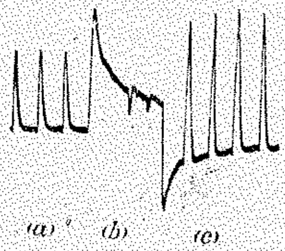

Fig. 77. Photographic record showing the effect of continuous stimulation in enhancing response (Pt). Each curve shows response (followed by recovery), the stimulus being kept constant throughout. The series of responses (*a*), enhanced to series (*c*) after continuous vibration (*b*).

Sometimes the wire gets into a very sluggish condition, when the response almost disappears; in other words, owing to some molecular modification, responsiveness is reduced from the normal positive value (by positive is meant that the acted wire becomes zinc-like or is zincoid) to zero. In these cases annealing or preliminary vibration are usually effective in transforming the sensitiveness from zero to the normal positive value.

Abnormal Response

But the modification of which I have spoken does not stop short of mere abolition of responsive power, but sometimes proceeds further, and actually reverses the sign of response—the excited wire becoming cuproid.

But even in such cases long-continued stimulation transforms the abnormal negative to the normal positive. I give below photographic records which exhibit this. In fig. 78, α, the transformation took place during continued vibration. To detect the point of transformation, I experimented with a platinum cell which exhibited the abnormal effect, and took a long series of records of responses to uniform stimulation acting at intervals of a minute. In the record (fig. 78, β) I have been able to catch the point or rather points of transition.

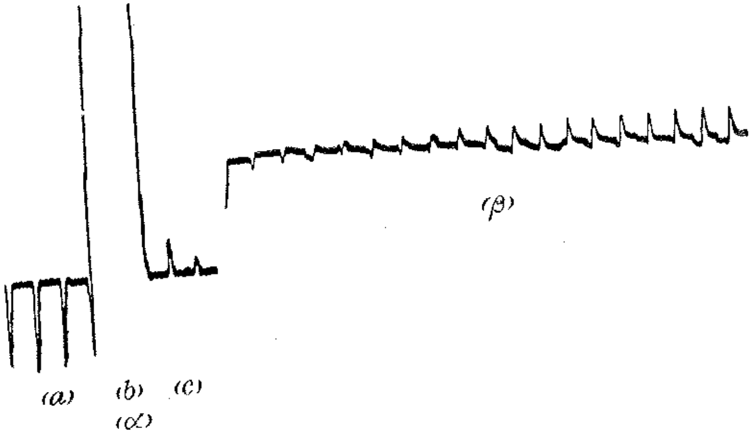

Fig. 78. (α) Abnormal negative (downward) response (*a*) of tin converted into normal positive (upward) response (*c*) after continued vibration (*b*).
(β) Shows points of transition from the abnormal negative to the normal positive (platinum).

Abnormal response of animal nerve.—It is interesting to note that similar abnormal response is also exhibited by animal nerve in condition of extreme sub-tonicity. This abnormal response of the nerve is also transformed into normal under continuous stimulation.

Returning to the response of metals we may distinguish the following typical cases. Beginning with the case of extreme molecular modification, we have (1) a condition which gives rise to the abnormal or negative response; after continued vibration the negative becomes less negative, and ultimately becomes converted into positive: (2) an irresponsive or neutral condition; vibration or annealing transforms it into positive: (3) a sluggish, feebly positive, becoming more and more positive after continued vibration: (4) a steady and permanent condition, when the responses are uniform: and lastly (5) when vibration is maintained for too long a time, the positive tends to become less positive, the responses decline—a state of things which is designated as fatigue.

Increased Electromotive Response under increased Intensity of Stimulus

When the intensity of stimulus is increased by increasing the amplitude of vibration, the electric res-

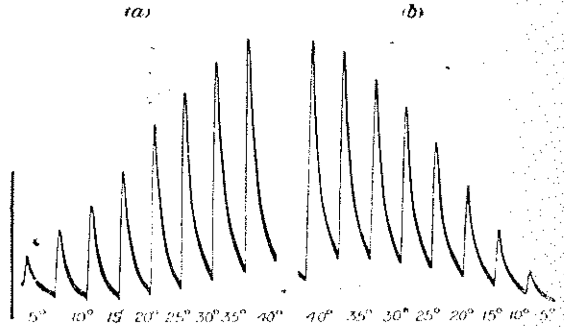

Fig. 79. Photographic records of responses (*a*) from 5° to 40°, (*b*) from 40° back to 5°. The vertical line=0·1 volt.

ponse undergoes an increase. The records given (fig. 79) are for amplitudes of vibration increasing from 5° to 40°, and decreasing from 40° to 5°. The successive stimuli are imparted at intervals of 1 minute. It will be noticed how the responses become enhanced under increasing stimulations.

Table I.—Showing the Increasing Electromotive Response under Increasing Amplitude of Vibration

Vibration amplitude.	Deflection. 23 dns.=0·1 volt.	
	Ascending.	Descending.
5°	5·5	5
10	13	12
20	25·5	26
25	33	32
30	39	39
35	43	43
40	47	48

It will also be noticed that whereas recovery is complete in 1 minute when the vibration amplitude is small, it is not quite complete within that time, when the vibration amplitude is large. Greater strain prolongs the period of recovery. Owing to want of complete recovery, the base line is tilted slightly upwards. This slight displacement does not materially affect the results, provided the shifting is slight. From other records taken through a greater range of stimulation, it appears that in a curve obtained with responsive electromotive variations as ordinates and amplitudes of vibrations as abscissæ, the first part of the curve is, generally speaking, slightly convex to the abscissa. This convexity

is more pronounced when feeble stimulation gives rise, as to be presently explained, to a response of opposite sign to that of the normal. The curve is straight in the middle and concave in the last part where the amplitude of response reaches a limit.

Effect of Sub-minimal Stimulus.—The response is of opposite sign to that of the normal, when the intensity of stimulus is sub-minimal. This characteristic effect I also find in the response of living tissues.

Maximum Effect

If instead of a single vibration of a given amplitude we superpose a rapidly succeeding series, the individual effects are added up and a maximum deflection is produced which remains practically constant as long as the vibration is maintained. A single ineffective stimulus thus becomes effective by the additive effect of several. Too long-continued vibration may cause fatigue, but during half a minute or so, the maximum effect in tin is very definite. For example, a single vibration of 5° gave a deflection of 3·5 divisions; the same when continued at the rate of four times per second gave a maximum deflection of eighteen divisions. A single vibration of 10° of the same wire gave a deflection of 4·5 divisions, but continued vibration gave the definite maximum of 37·5 divisions. I give below a curve (fig. 80) exhibiting the maximum effects for different amplitudes of vibration.

Hysteresis.—Allusion has already been made as to the increased sensitiveness conferred by preliminary vibration. Being desirous of finding out in what manner this is brought about, I took a series of observations for an entire cycle, that is to say, a series of observations were taken for maximum effects, starting from 10° and ending in 100°, and backward from 100° to 10°. Effect of hysteresis is very clearly seen (fig. 80, A); there is a considerable divergence between the forward and return curves, the return curve being higher of the two. On repeating the cycle several times, the divergence becomes much reduced, the wire acquires a more constant sensitiveness.

Effect of Annealing.—I repeated the experiment with the same wire, after pouring hot water and allowing it to cool to the old temperature. It will be seen from the cyclic curve (fig. 80, B), (1) that the sensitiveness has become very much enhanced; (2) that there is relatively less divergence between the forward and return curves. Even this divergence practically disappeared at the third cycle, when the forward and backward curves coincided (fig. 80, C). The above results show in what manner the excitability of the wire is enhanced by purely physical means.

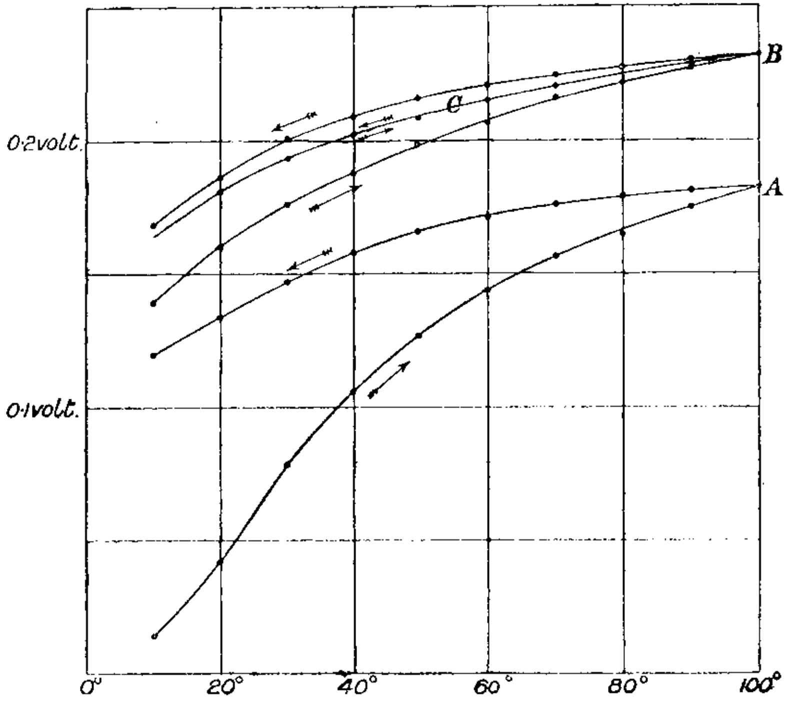

Fig. 80. Cyclic curves for maximum effects due to increasing and decreasing amplitudes of vibration. A, fresh wire; B, after annealing; C, the same after three cycles. Abscissa represents the amplitude of vibration; the ordinate represents the corresponding electromotive variation.

It is very curious to notice that the substitution of dilute Na_2CO_3 solution as electrolyte produces results very similar to that produced by annealing; that is to say, not only is there a great enhancement of sensitiveness, but there is also a reduction of hysteresis. Another curious point is that, whereas with ordinary fresh wire the addition of Na_2CO_3 greatly enhances the sensitiveness, after the wire has been annealed there is comparatively little further increase of sensitiveness due to the addition of the reagent.

Effect of Chemical Reagents

I reproduce photographic records of a few typical cases which will graphically illustrate the influence of chemical reagents. The mode of procedure is as follows. The cell is filled with water, and photographic records are taken of responses to single vibrations of constant amplitude, applied to one of the two wires at intervals of 1 minute. The responses are found to be uniform. Chemical reagents are now added, and responses obtained as before. These exhibit either an increase or a diminution, depending on the exciting or depressing nature of the reagent. It is also quite easy to obtain duplicated results by alternately vibrating the A and B wires. Uniform responses, alternately positive or negative, are first obtained; after the addition of reagent *both* are found to exhibit either an increase or a diminution. As has been said before a very high external resistance, varying from 1 to 5 megohms, is interposed in the external circuit, the slight variation of internal resistance of the cell due to the addition of the reagent being thus rendered quite negligible compared with the total resistance of the circuit. That there is no appreciable variation in the total resistance can be independently verified by applying a known electromotive force before and after the addition of the reagent, when the resulting deflection is found to be the same in the two cases. The deflections are thus simply proportional to the responsive electromotive variations.

Chemical Excitants.—The following record (fig. 81) exhibits the increased response due to the action of Na_2CO_3 on Pt. Another record shows an exactly similar effect on tin. The record of effect was taken two minutes after the application. Other records taken immediately after, show that the enhanced responsiveness takes place gradually with time.

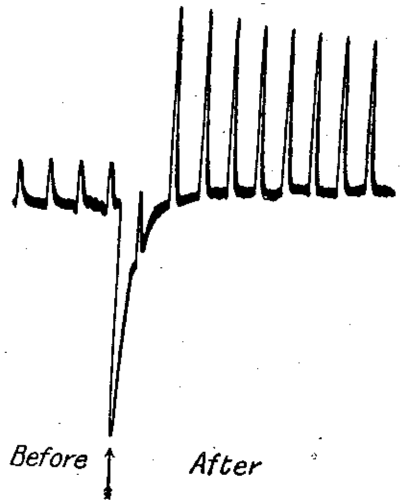

Fig. 81. Enhanced response by the action of Na_2CO_3 solution on platinum. The intensity of stimulus is kept constant throughout. Records to the left show the responses before, and those to the right after, the application of Na_2CO_3.

Depressants.—Reagents, like KBr (10 per cent.), produce a depression in the response. There are again others which abolish the response almost completely, for example, 3 per cent. KHO solution (fig. 82, *c*). One of the most effective reagents which abolishes the response is oxalic acid. The depressing effect of this reagent is so great that a strength of 1 part in 10,000 is often sufficient to produce an abolition of response.*

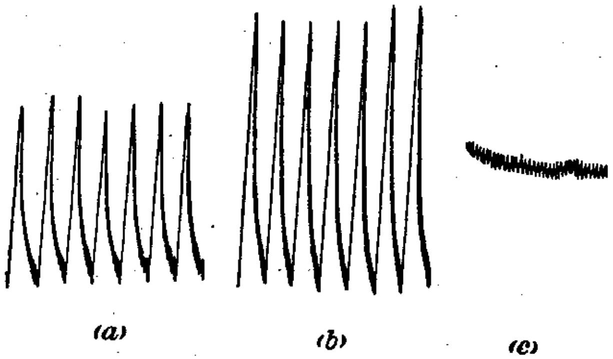

Fig. 82. Records showing the opposite effects of weak and strong solutions. (*a*) Normal response; (*b*) increased response due to addition of 0·3 per cent. KHO; (*c*) abolition of response by 3 per cent. KHO.

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* The various phenomena connected with the response in inorganic substances—the negative variation—the relation between stimulus and response—the increased response after continuous stimulation—the abnormal response converted into normal after long-continued stimulation—the diphasic variation—the increase of response by stimulants, decrease by depressors, and abolition by "poisons," so-called—all these are curiously like the various response phenomena in living tissues. A complete account of the mutual relation between the two classes of phenomena will be found in my work "The Response in the Living and Non-living."

Opposite Effects of strong and feeble dose.—The most curious effect is that exhibited by the same reagent when the strength of solution is varied. This is clearly seen in record (fig. 82), in which (*a*) gives the normal response in water; (*b*) shows the enhancement of response by a highly dilute solution of KHO, 3 parts in a thousand. The response was completely abolished by a stronger solution, 3 parts in a hundred (fig. 82 *c*).

Effect of "poisons."—Certain agents like oxalic acid cause a total abolition of response, like the action of poisons on living tissues.

The facts described above appear to show that the enhancement or depression of response may, at least to a considerable extent, be due to the increase or diminution of molecular mobility. With a given stimulus, the height of response and the form of the response curve is determined by the element of molecular friction. In connection with this, it is instructive to observe the records of vibrations of a torsional pendulum, the friction being gradually increased by immersing the pendulum in a viscous fluid. The various types of response-curves in metals are found to be very similar to the above.

Of these I give an interesting example. With moderate friction the successive curves obtained with the pendulum are like those given in the left of fig. 83 (*a*). With increased friction the height of the curve is diminished, the maximum is reached later, and the recovery becomes much prolonged like the curve to the right. With still greater friction there is an arrest of recovery.

It would appear as if the reagents which abolish response in metals produce a similar molecular arrest.

The following photographic records seem to lend support to this view. If the oxalic acid be applied in large quantities, the abolition of response is complete; but on carefully applying just the proper amount, I find that the stimulus evokes a responsive electric variation which is less than the normal, and the period of recovery is very much prolonged from the normal 1 minute before to 5 minutes after the application of the reagent. In the lower record (fig. 83) the normal response and recovery is seen in the left record. After the application of oxalic acid the record to the right shows a pronounced arrest, *i.e.*, there is now no recovery. Note also that the maximum is attained much later. Stimuli applied after the arrest produce no effect, as if the molecular mechanism had become locked up.

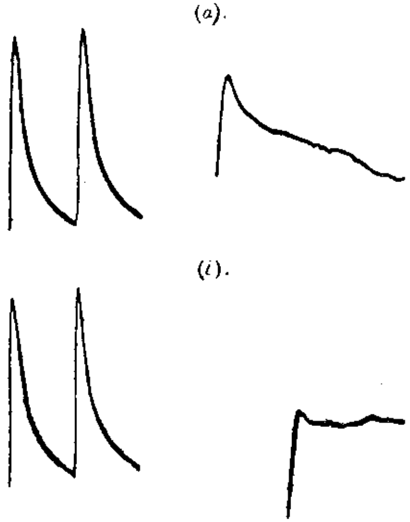

Fig. 83. Photographic records showing the effect of "molecular arrest." The two curves to the left of each set show the normal response; curve to the right in (*a*) shows partial and in (*b*) complete arrest.

Conclusion

1. Molecular disturbance produced by mechanical stimulation gives rise to an electromotive response. In the majority of cases, under normal conditions, the responsive electrical current in a wire is from the less to the more stimulated.

2. Response may be obtained by (1) method of block, (2) by methods of negative or positive variation.

3. The electromotive response disappears on the cessation of stimulus.

4. The intensity of the electrical response is modified by the molecular condition of the wire. Annealing, or previous stimulation enhances the electric response.

5. Abnormal response due to molecular modification is transformed into normal by previous stimulation.

6. The intensity of electric response is increased with increasing intensity of stimulation.

7. In a curve showing the relation between intensity of stimulus and resulting response, the first part is slightly convex to the abscissa, the second is approximately straight, and the third concave. The response tends to reach a limit.

8. Minimally effective stimulus becomes effective by summation of stimuli. A maximum effect is produced, determined by the intensity of individual stimulation.

9. Hysteresis is exhibited in cyclic curves. The forward and return curves tend to coincide after several cycles. Previous annealing reduces hysteresis, and after one or two cycles the wire assumes a constant sensitivity.

10. Chemical reagents may profoundly modify the electric excitability. Some of them increase the excitability, while others depress or abolish it.

11. The effect of a feeble dose is often opposite to that of a stronger dose.

12. By touching different points of the same wire with different reagents, the excitability of these portions are rendered unequal. Hence a responsive electromotive variation is obtained by stimulating the wire as a whole. The current in the wire is from the less to the more excitable.

13. This method enables the detection of invisible traces of physico-chemical change in a wire.

14. Chemical reagents not only change the excitability but also the quickness of response. Two points having two different rates thus give diphasic and other interference effects.

(*Proc. Roy. Soc. May* 1902.)

XXI

ELECTRIC RESPONSE IN ORDINARY PLANTS UNDER MECHANICAL STIMULATION

Discovery of the similarity of response in inorganic substances and in animal tissues led me to the investigation of responsive phenomena in the intermediate region of life of plants.

The action of stimulus on living substances is usually detected by two different methods. In the case of motile organs, stimulus causes a change of form. Mechanical response may thus be obtained in a contractile tissue such as a muscle. But in others, nerve for example, stimulus causes no visible change; the excitation of the tissue may, however, be detected by characteristic electromotive changes. The advantage of the electric mode of detection of response is its universal applicability. In cases where mechanical response is available, as in the muscle, it is found that records of mechanical and electrical responses are very similar to each other.

The intensity of electrical response in animal tissue is modified by the physiological activity of the tissue. When this activity is in any way depressed, the intensity of electrical response is also correspondingly diminished. When the tissue is killed, the electrical response disappears altogether.

Burdon Sanderson, Munck, and others found electric response to occur only in sensitive plants. I wished to find out whether the responsive electric variation was confined merely to organs of plants which exhibit such remarkable mechanical movements, or whether it was a universal phenomenon characteristic of all plants and of all their different organs. My attempt was moreover directed in determining throughout the whole range of response phenomena a parallelism between the animal and the vegetable. That is to say, I desired to know, with regard to plants, what was the relation between the stimulus and response; what were the effects of superposition of stimuli; whether fatigue was present, and in what manner it affected the response; what were the effects of extremes of temperature; whether chemical reagents exercised any influence on the plant-response, as anæsthetics and poisonous drugs affected the responses of nerve and muscle.

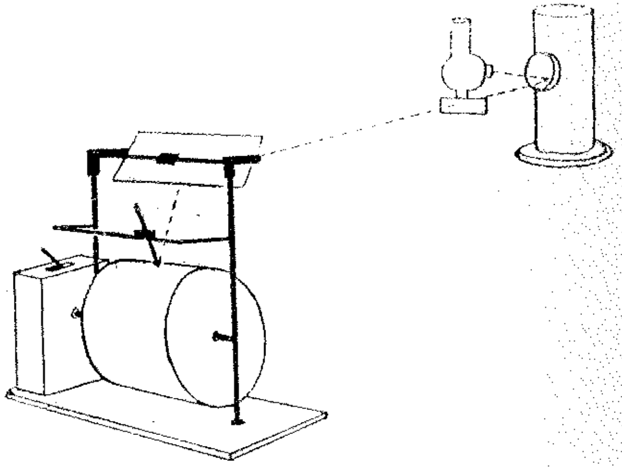

Fig. 84. Response Recorder.

Experimental Arrangements

The galvanometer used is a sensitive dead-beat D'Arsonval. A current $1/10^9$ ampere gave a deflection of 1 mm. at a distance of 1 metre.

The Response Recorder.—In these response-curves the ordinate represents the intensity of E. M. variation, and the abscissa the time. The curves are obtained directly, by tracing the excursion of the galvanometer spot of light on a revolving drum. The drum, on which is wrapped the paper for receiving the record, is driven by clockwork (fig. 84). Different speeds of revolution can be given to it by adjustment of the clock-governor, or by changing the size of the driving-wheel. The galvanometer spot is thrown down on the drum by an inclined mirror. A stylographic pen attached to a carrier rests on the writing surface. The carrier slides over a rod parallel to the drum. On stimulation, the resulting excursion of the spot of light is followed by moving the carrier which holds the pen; after the cessation of stimulus the excitatory effect slowly disappears, and the galvanometer spot returns gradually to its original position. The response and recovery are thus directly traced on the recording surface. We can calibrate the value of the deflection by applying a known electromotive force and noting the deflection which results. The speed of the clock is previously adjusted so that the recording surface moves exactly through, say, one inch a minute; this speed can, however, be increased to suit any particular experiment. Very accurate records can thus be obtained in a very simple manner. A large number of records might be taken by this means in a comparatively short time.

Photographic Recorder.—The records may also be made photographically. A clockwork arrangement moves a photographic plate at a known uniform rate, and a curve is traced on the plate by the moving galvanometer spot of light. The records given in this paper are accurate reproductions of those obtained by one of these two methods.

Graduation of the Intensity of Stimulus

The important conditions for securing quantitative results are (1) the maintenance of uniform intensity of stimulation in certain experiments and (2) the graduated increase of intensity in others.

Stimulus of torsional vibration.—I find that torsional vibration affords a very effective method of stimulation. The plant-stalk may be fixed at one end, the other end being held in a tube provided with clamping jaws. A rapid torsional to-and-fro vibration can now be imparted to the stalk by means of the handle H. The amplitude of vibration, which determines the intensity of stimulus, can be accurately measured by means of a graduated circle. The plant chamber and the vibrational stimulator is shown in fig. 85.

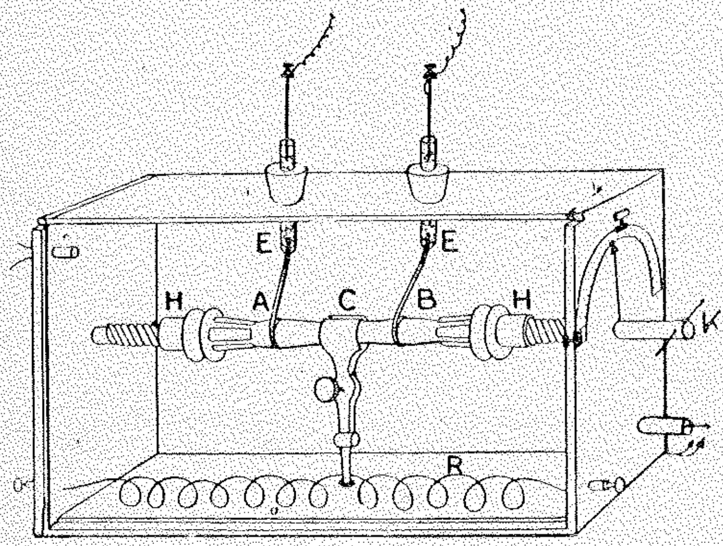

Fig. 85. The plant chamber. Amplitude of vibration which determines the intensity of stimulus is measured by the graduated circle seen to the right. The glass chamber is air-tight. The plant is clamped in the middle by C which acts as a block. Temperature is regulated by the electric heating-coil R. For experiments on anæsthetics, vapour of chloroform is blown in through the side tube.

Intensity of Stimulus dependent on Amplitude of Vibration

A block is produced by clamping the plant in the middle at C; increased stimulation is found to occur in the tissue by increased amplitude of vibration.

The Physiological Character of Response

I now proceed to demonstrate that the response given by the plant is physiological and that it affords an accurate index of the vital activity of the plant. For it will be found that whatever tends to exalt or depress this activity also tends to increase or diminish the intensity of electric response.

The test applied by physiologists, in order to discriminate as to the physiological nature of the response consists in observing the effects of anæsthetics, poisons, and exceedingly high temperatures, all of which are known to depress or destroy the activity of life.

Effect of Anaesthetics and Poisons.—I took 30 leaf-stalks of horse-chestnut, and divided them into 3 batches, of 10 each. One batch was kept in water, to serve as control experiment, another in chloroform water, and the third in a 5 per cent. solution of mercuric chloride.

Average response of stalks kept in water=23 divisions.

Average response of stalks kept in chloroform=1 division.

The response of stalks kept in poisonous mercuric chloride was completely abolished.

Effect of High Temperature.—A leaf-stalk is taken, and using the block method strong responses are obtained at both ends A and B. The stalk is now immersed for a short time in water at 60° C. After this treatment

the responses are found to be completely abolished. As all the external conditions were the same in the two series of experiment, the only difference being that in one the stalk was alive, and in the other killed, we have here a further and conclusive proof of the physiological character of electric response in plants.

The same facts may be demonstrated in a still more striking manner by first obtaining two similar but opposite responses in a fresh stalk at A and B, and then killing one half, say B, by immersing that half in hot water. The stalk is replaced in the apparatus; repetition of the experiment shows that whereas the A half gives strong response, the end B gives none.

Uniform Responses

Uniform responses may be obtained with certain plants in a vigorous condition, and when sufficient period of rest is allowed for complete recovery. The record given below shows the remarkable uniformity of response given by radish. The response of plant is by the induced galvanometric negativity of the excited tissue just as in the tissue of the animal.

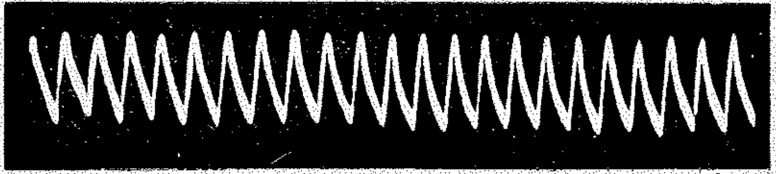

Fig. 86. Uniform responses (Radish).

Fatigue

The responses however exhibit fatigue by shortening the intervening period of rest. The first four responses in fig. 87 show that there is a complete recovery of the tissue one minute after the application of the stimulus.

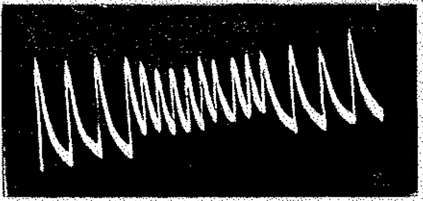

Fig. 87. Appearance of fatigue in plant under shortened period of rest.

The molecular condition is exactly the same at the end of the recovery as at the beginning of stimulation; the second and succeeding response-curves therefore are exactly similar to the first, *provided sufficient interval in each case has been allowed for complete recovery.*

The rhythm was next changed and stimuli of the same intensity as before applied at intervals of half a minute, instead of one. It will be noticed that these responses in the second part appear much feebler than those in the first set, in spite of the equality of stimulus. The original rhythm of one minute was now restored and the succeeding curves at once show restoration of the original amplitude of response.

Increased Response under increasing Stimulus

I will now show that the electric response is not merely a qualitative phenomenon, but that increased intensity of stimulus always gives rise to a definite increase in the amplitude of response.

In order to obtain the simplest type of effects, not complicated by secondary phenomena, it is necessary

to choose specimens which exhibit little fatigue. Having obtained such a specimen I took records of responses for increasing stimuli caused by increasing amplitudes of vibration.

In the record given (fig. 88) the amplitude of vibration was increased from 2°·5 to 12°·5 by steps of 2°·5 (cauliflower-stalk). It will be noticed the remarkably definite manner in which the response increases with the stimulus. The rise is at first rapid, but with high intensities of stimulus there is a tendency for the response to approach a limit.

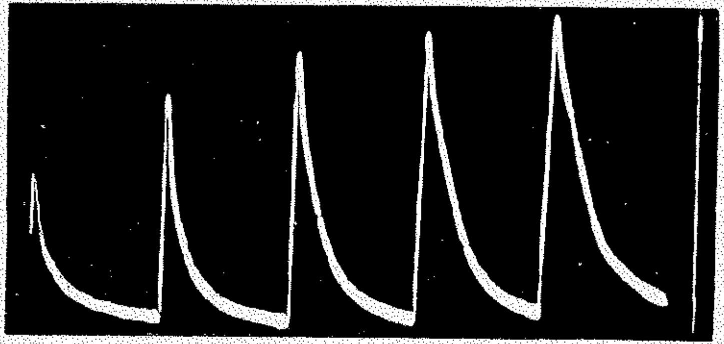

Fig. 88. Increasing responses to increasing vibrational stimuli; the vertical line to the right represents ·1 volt.

Superposition of Stimuli

Additive effect.—There is apparently little or no response when the stimulus is feeble. But even a subminimal stimulus, though singly ineffective, becomes effective by the summation of several. This is shown in fig. 89, where the first record *a* is the response to a feeble stimulus, and the second *b* is the response to the same stimulus repeated in quick succession, thirty times.

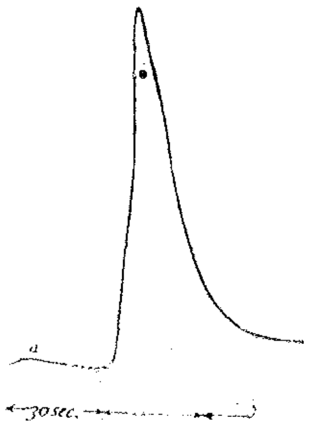

Fig. 89. Additive effect of singly ineffective stimuli in plant.

Effect of Steam

The plant was mounted in a chamber into which steam could be introduced. I had chosen a specimen which gave regular responses. On the introduction of steam, with consequent rise of temperature, there was a transitory augmentation of excitability. But this quickly disappeared, and in five minutes the response disappeared with the death of the plant (fig. 90).

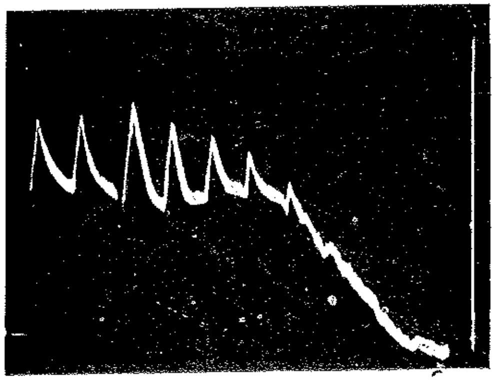

Fig. 90. Effect of steam in abolishing response with death of plant. The two records to the left give responses at 20° C., after which steam was introduced.

Effects of Anaesthetics and Poisons

The most important test by which vital phenomena are differentiated is the influence of narcotics and poisons on response. I have already shown how plants which previously gave strong response, did not, after application of an anæsthetic or poison, give any response at all. In those cases it was the last stage only that could be observed. But it appeared important to be able to trace the growing effect of anæsthetisation or poisoning throughout the process.

Effect of Chloroform.—The mode of experiment was (1) to obtain a series of normal responses to uniform stimuli, applied at regular intervals of time, say one minute, the record being taken the while on a photographic plate. (2) Without interrupting this procedure, the anæsthetic agent, chloroform vapour, was

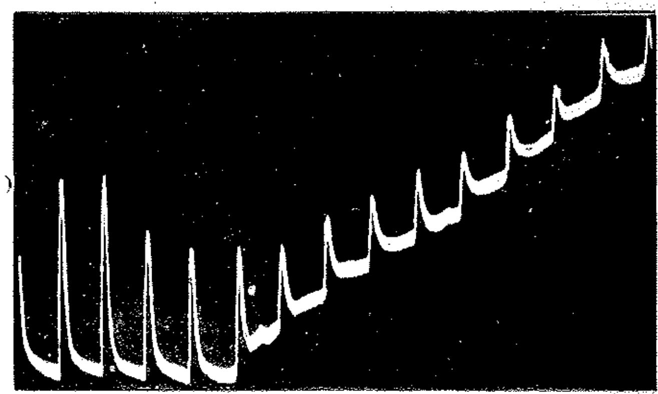

Fig. 91. Effect of chloroform.

blown into the closed chamber containing the plant. It will be seen how rapidly chloroform produced depression of response which afterwards culminated with death and abolition of response (fig. 91).

Exactly similar effects were obtained with chloral, also with formalin. These were applied in the form of solution on the tissue at the two leading contacts.

It has been shown that the electric response is a faithful index of physiological action and that such a response is given by all plants and by their different organs. It has also been shown that in the matters of response by induced galvanometric negativity, of modification of response by high and low temperatures, they are strictly correspondent to similar phenomena in muscle and nerve. Judged by the final criterion of the effect produced by anæsthetics and poisons, these electric responses in plants fulfil with animal tissues the test of vital phenomenon.

The electro-physiological investigation on plants will undoubtedly throw much light on the response phenomena in the animal. With animal tissues, experiments have to be carried on under many great and unavoidable difficulties. The isolated tissue, for example, is subject to unknown changes inseparable from the approach of death. Plants, however, offer a great advantage in this respect, for they maintain their vitality unimpaired during a very great length of time. In animal tissues, again, the vital conditions themselves are highly complex. The essential factors which modify response can, therefore, be better determined under the simpler conditions which obtain in plant life.

(*Journal Linn. Soc., Vol. XXXV*, 1902.)

XXII

THE QUADRANT METHOD OF RESPONSE TO STIMULUS OF LIGHT

In addition to the method of electromotive variation, I succeeded in perfecting an independent means for recording the response of plants by the variation of its electric resistance. The living tissue excited by any mode of stimulation—mechanical, electrical or photic—responds by a diminution of resistance. A new method of resistivity variation of extreme delicacy will now be described by which the response of the leaf to the stimulus of light can be recorded.

The principle of the method will be understood from the diagram given at the lower end of figure 92, which represents a leaf blade of *Tropaeolum* in which its four quadrants P, Q, R, S, serve as the four arms of a Wheatstone Bridge. The diagonal connections are made with the battery and the galvanometer respectively. The three contacts with the leaf may be fixed, and the fourth moved slightly to the right or to the left till an exact balance is obtained in darkness, when PQ=RS. One of the pairs of opposite quadrants P and Q is shaded by a double V-shaped screen. Exposure of the leaf to light produces a variation of resistance not of one, but of two opposite arms of the bridge R and S; the upsetting of the balance is thus due to the *product* of the variations of resistance in the two opposite quadrants. The responsive galvanometer deflection is found to be very large indicating a diminution of resistance in the quadrants stimulated by light. The double V-shaped screen is next turned through 90° ; the quadrants P and Q are now exposed to light, and R and S shaded from it. The resulting upset of the balance and the galvanometer deflection is now in an opposite direction.

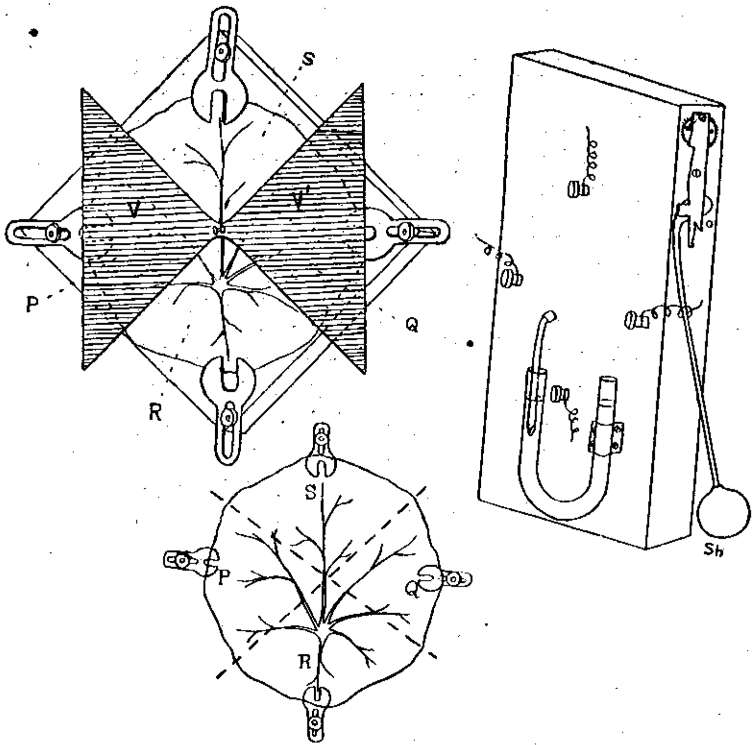

Fig. 92. The Quadrant Method of response by variation of electric resistance. Two opposite quadrants of the leaf are shaded. Electric connections are made at the *junctions* of the quadrants and not at the middle as shown in figure.

The reliability and the sensitiveness of the Quadrant Method may thus be tested by obtaining equal and opposite responses under alternate illumination of the two pairs of quadrants ; the test in confirmation of the above will be found in records given in figure 93.

After securing exact balance, the double V-shaped screen is kept fixed, and the leaf mounted in a rectangular dark chamber closed except at the front, which carries a photographic shutter by which one pair of quadrants is exposed to light for a definite duration. The electric connections with the leaf are led to four binding screws ; the petiole protruding from the box is dipped in an U-tube filled with water (*cf.* right-hand illustration of fig. 92).

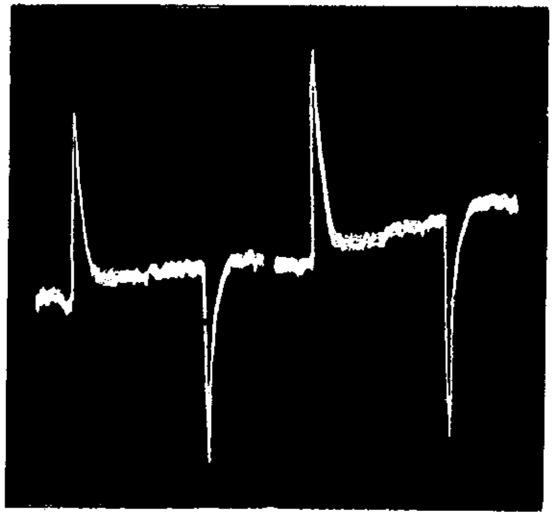

Fig. 93. Equal responses in opposite directions by alternate illumination of the two pairs of quadrants.

The source of light is an arc or an incandescent lamp, placed inside a lantern, the condenser of which sends a parallel beam of light. A rectangular glass trough filled with alum solution is interposed in the path of light to absorb the heat rays. The duration of exposure is varied according to the sensitiveness of the specimen ; the usual period of exposure is about 20 seconds.

RESPONSE TO LIGHT FROM A SINGLE SPARK

The extreme sensitiveness of the quadrant method is demonstrated by the record given in figure 94.

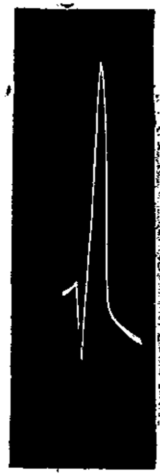

Fig. 94.

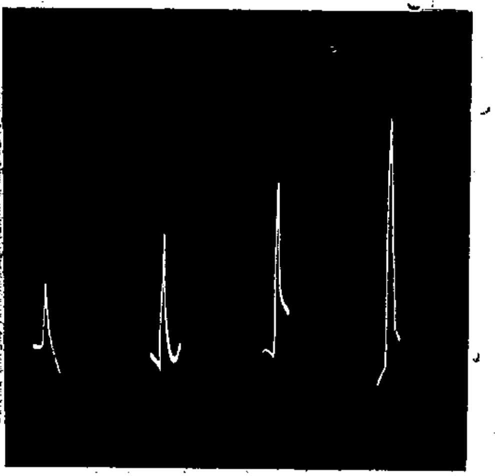

Fig. 95.

Fig. 94. Response to light from a single spark.
Fig. 95. Effect of stimulus of light increasing in the ratio of 1 : 3 : 5 : 7.

The duration of a spark-discharge of a Leyden Jar may be regarded as of the order of hundred thousandth part of a second. The discharge took place at a distance of 15 cm. from the leaf and the response is seen to consist of a preliminary positive twitch followed by a large negative response, indicative of normal diminution of resistance. The leaf exhibited a complete recovery.

Effect of increasing Intensity of Light

The arc lamp is taken out of the lantern, and the diverging beam employed for the following experiment. As the intensity of light varies as the square of the distance, suitable marks were made on the scale fixed on the table, so that the intensity of light incident on the leaf was increased in the proportion of 1 : 3 : 5 : 7 by bringing the arc nearer the leaf at the particular distances marked on the scale. The duration of exposure was kept the same.

The responses under increasing intensities of light are seen in figure 95. The resistance is seen to undergo a diminution with the increasing intensity of stimulus.

Effects of Stimulants and Depressants

The responses are appropriately modified by stimulating or depressing agents. Dilute vapour of ether, for example, increases the excitability and enhances the amplitude of response. Strong dose of chloroform, on the other hand, causes depression and death as indicated by gradual diminution and final abolition of response.

The results of other investigations, fully described elsewhere, show that external stimulation gives rise to two definite protoplasmic reactions, which may be described as the A- and the D-effects. The A-effect, usually induced by sub-minimal stimulus, finds outward expression, by induced expansion, increase of turgor, enhancement of the rate of growth, galvanometric positivity and increase of electrical resistance. The D-effect (predominantly induced under stimulus of moderately strong intensity) is outwardly manifested, on the other hand, by contraction, diminution of turgor, diminished rate of growth, galvanometric negativity and diminution of electric resistance. Under very strong stimulation the response tends to become multiple. The following table shows the parallel effects exhibited by diverse modes of response.

Table showing parallelism in different modes of response

External change	Mechanical response	Variation of growth	Electromotive response	Resistivity variation
Sub-minimal stimulus	Expansion; erectile response	Acceleration of growth	Galvanometric positivity	Increase of resistance
Moderate stimulus	Contraction and fall of leaf	Retardation of growth	Galvanometric negativity	Diminution of resistance
Strong stimulus	Multiple response	Multiple response	Multiple response	Multiple response
Depressants	Diminished response	Retardation of growth	Diminished response	Diminished response
Stimulating agents	Enhanced response	Acceleration of growth	Enhanced response	Enhanced response

(*Life Movements in Plants, Vol. IV*, 1923.)

XXIII

ON A VEGETABLE PHOTO-ELECTRIC CELL

When light is incident on the sensitive pulvinus of *Mimosa pudica*, the response is by contraction and the resulting fall of the leaf. A diminution of electric resistance of tissues of plants under stimulation has also been demonstrated in the previous paper. The electromotive response of *galvanometric negativity*, under the excitatory action of light, has previously been demonstrated in my work on *Comparative Electro-physiology*. I here describe a new and interesting method for this demonstration.

Normal Response to Light

For obtaining the normal response, we take a vigorous leaf and pin it on a paraffined block of wood. Two pieces of thin muslin in connection with non-polarisable electrodes are spread over two areas of the leaf A and B; when these pieces of muslin are moistened with normal saline, they become practically transparent. When light from an arc lamp is thrown on A, that area becomes galvanometrically negative and the responsive current flows in the direction GAB. Light thrown on B (A being shaded) causes a response in the opposite direction, (left illustration fig. 96).

The fact, that the electromotive response under light is the same as that under a different mode of stimulation such as mechanical, is demonstrated as follows. The moist piece of cloth on A is rubbed against the surface of the leaf by means of a glass rod; or the surface is struck with a glass hammer. In both these cases, A end of the leaf becomes galvanometrically negative, the direction of the current of response being the same as when A is stimulated by light.

Having given a simple demonstration of the fundamental reaction, I describe the photo-electric cell made of two pieces of leaf. In the experiment just described, the resistance of the circuit is very great, on account of the high resistance of the two non-polarisable electrodes, and the resistance offered by the leaf. The non-polarisable electrode, moreover, is a source of trouble; an attempt was therefore made to discard it, and employ other means for diminishing the resistance of the circuit. For the following experiments we employ the leaf of *Musa sapientum* which is divided into two longitudinal halves by a slit along the thick midrib. Two pieces of leaves are thus obtained about 10×10 cm. which are hung parallel and separated from each other in a rectangular glass vessel filled with normal saline; the distance between the two leaves is 3 cm. Two gold wires are thrust through the length of the two divided midribs; they serve as external electrodes of the photo-voltaic cell, which lead to the galvanometer G. The glass trough is placed inside a rectangular wooden chamber with two hinged doors on opposite sides, by which the leaf A or B could be alternately exposed to light (fig. 96). When the doors are closed, A and B are in darkness; they are practically iso-electric, there being no current in the galvanometer. But exposure of A to light gives rise to a difference of potential between A and B, A becoming galvanometrically negative, the resulting deflection being in one direction. Exposure of B gives rise to a responsive deflection in the opposite direction. The two leaves serve as the two plates in a voltaic cell; but unlike ordinary voltaic cell with elements of different metals, the two plates of the vegetable cell are made of two halves of the same leaf, the electromotive force being generated by the excitatory action of light on one of the two half leaves. The advantages of this method of obtaining electromotive response are: (1) that the troublesome employment of the non-polarisable electrodes with their high resistance is dispensed with; (2) that the area of the surface of the leaf exposed to light is considerably increased; (3) that the electric resistance of the circuit is greatly decreased, since the interposed resistance is that of normal saline about 3 cm. thick with a broad section of 100 square cm.; and (4) that alternate and opposite responses may be obtained by successive exposures of the two leaf-plates to the parallel beam of an arc lamp, this being easily secured

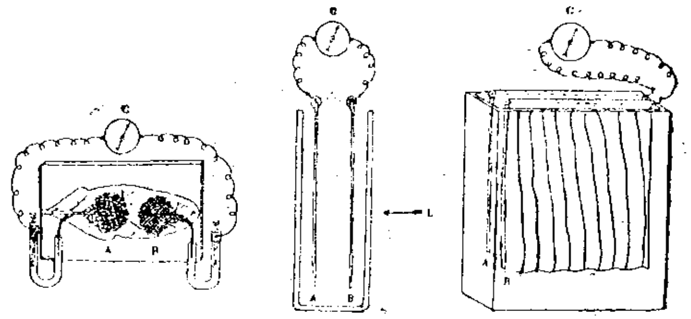

Fig. 96. Diagrammatic representation of a vegetable photo-electric cell. The first illustration shows electric connections with two portions of the leaf A, B, by non-polarisable electrodes. The second and third illustrate side and front views of the photo-voltaic cell made of two half-leaves.

by turning the rectangular plant chamber round a revolving base.

Response of the Leaf to Light

The photo-voltaic cell thus constructed is stimulated by light from an arc lamp which passes through a trough of alum solution for absorption of the heat rays. Successive exposures are made for 10 seconds and records obtained on a moving photographic plate. The normal responses are uniform, exhibiting induced galvanometric negativity as seen in the up-curves. On the cessation of light there is a complete recovery; the recovery shows in fact, an overshooting towards galvanometric positivity from which it returns almost to the original zero position before stimulation (fig. 97). The records indicate the existence of dual reactions, a negative variation or D-effect followed by a positive variation or the A-effect.

Positive Response to Light

Some observers have obtained with green leaves a response of galvanometric positivity. The results of following investigation offer an explanation of the apparent anomaly. I have shown elsewhere that a positive response occurs under a stimulus below the critical intensity, and that this critical point is low in highly excitable tissues, whereas it is relatively high in others which are less excitable. The excitability, I find, is modified by the age and vigour of the specimen. It is very considerable at moderately young age, being feeble when the tissue is either very young or very old. The same stimulus which evokes a negative response in a vigorous middle-aged leaf may, therefore, be expected to give rise to a positive response in a very young leaf or in a leaf which is becoming yellow with age.

The above anticipations have been found verified in the following experiments. In figure 98 is seen the positive response of a very young leaf of Musa; the next figure shows similar positive response given by a very old leaf. There is an additional factor, to be presently described, which also tends to induce a positive response.

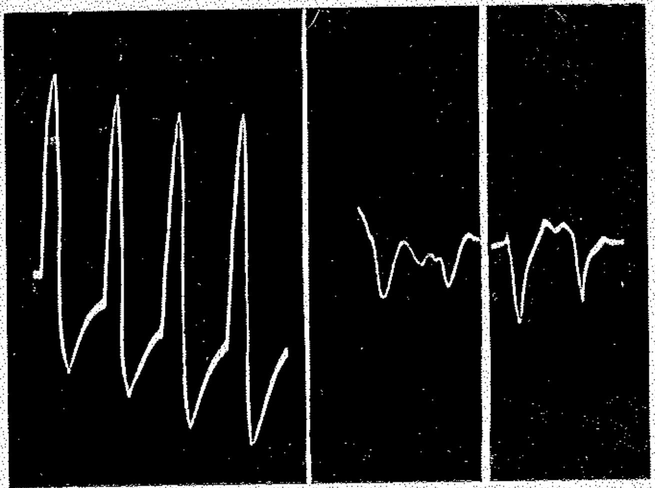

Fig. 97. Fig. 98. Fig. 99.

Fig. 97. Normal electromotive response in a vigorous specimen. Note the transient positive after-effect.

Figs. 98 and 99. Abnormal positive response in a very young and in a very old specimen.

Effect of Increasing Duration of Exposure

The reaction under light, is within limits, proportional to the quantity of light, that is to say, on intensity of light multiplied by duration. The effect of increasing intensity of light has already been shown (*cf.* fig. 95). When the intensity is maintained constant, the amplitude of response undergoes an increase with the increased duration of exposure (fig. 100). But this increase does not go on indefinitely, for the continuous action of light causes a maximum negative response beyond which a decline sets in. It is probable that this is due to an opposing element which tends to neutralise the normal excitatory D-effect. The existence of this opposing A-reaction has already been seen in the transient after-effect in figure 97. Other results which I obtained, show that stimulus induces, in general, both the D- and A-effects; in excitable specimens the D-effect is predominant and therefore, masks the A-effect; the positive A-effect is, however, exhibited under feeble or even as an after-effect of strong stimulation.

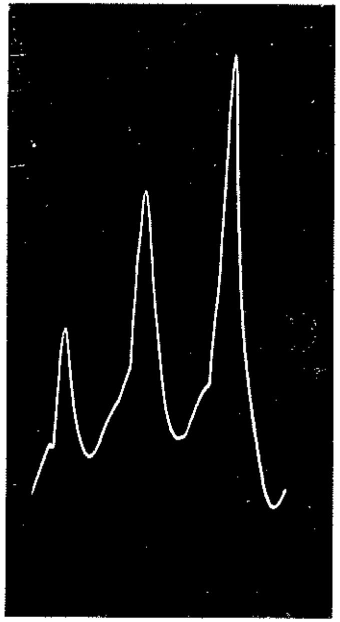
Fig. 100. Effect of increasing durations of exposure of 5, 10 and 15 seconds.

Certain conditions, moreover, are specially favourable for the exhibition of the A-effect. When the green leaf has an abundant supply of chlorophyll, the photo-synthetic process of building up becomes specially marked. I have thus obtained under the action of light, a positive response with the green leaf of *Luctuca sativa* in which chlorophyll is present in great abundance.

The fact that positive response is associated with assimilation is proved by my experiments on photo-electric response of water plants. This building up process by photosynthesis is here independently demonstrated by profuse evolution of oxygen. These aquatic plants exhibit marked positive electric response during strong illumination, recovery taking place on the cessation of light (fig. 101).

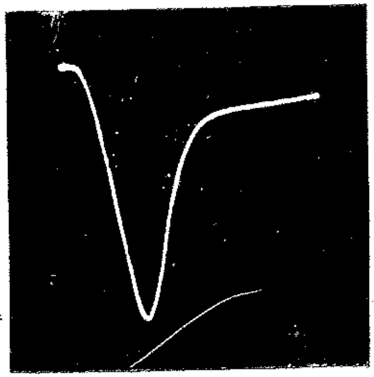
Fig. 101. The positive electric response of Hydrilla.

Effect of Continued Action of Light

The positive element in the response may be indirectly demonstrated even in the normal *Musa* leaf. In figure 102 is seen the effect of continuous action of light which at first exhibits the predominant negative attaining a maximum; the positive element now begins to increase with the duration of light and causes a reversal; at a certain stage, the two elements, D and A, balance each other, the resulting response becoming horizontal, On the stoppage of light, the antagonistic A element ceases to be active, while D appears to be persistent. The result is a sudden unmasking of the negative, hitherto held in balance during exposure to light. A negative response with subsequent recovery thus occurs on the cessation of light.

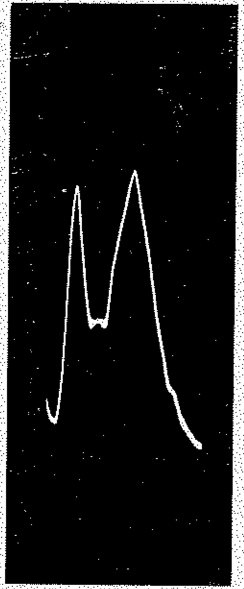

Fig. 102. After-effect of light. The maximum negative is opposed by growing positive and the balance attained is seen in the horizontal portion of the curve. Stoppage of light causes the unmasking of the negative followed by recovery.

The responses of *Musa* and of actively assimilating *Hydrilla* are seen to exhibit characteristic differences on account of the relative predominance of the D- or A-effect. In *Musa*, D is predominant, A being exhibited either as a positive after-effect or by the overshooting of response in the positive direction. In an actively assimilating *Hydrilla* plant, on the other hand, A is predominant and the response is positive. In less vigorous *Hydrilla* the positive becomes masked by the negative, when the resultant response appears to be similar to that of *Musa*.

(*Life Movements in Plants, Vol. IV*, 1923.)

XXIV

THE PHOTOSYNTHETIC RECORDER

The incessant activities of life require expenditure of energy that has been previously stored by the organism. Taking, for example, the rise of sap, the ceaseless pumping activity of certain propulsive tissue raises enormous quantities of water to a considerable height. The energy of doing this work resides in the breakdown of complex chemical substances in internal combustion or respiration. The loss of energy must be restored by absorption and storage of energy from outside.

This is secured in green plants by photosynthesis, carbon being fixed for nutrition of the plant with the help of sunlight.

The carbon-assimilation of plants is of great theoretical interest as an example of the simplest type of assimilation. The plant absorbs the carbonic acid, CO_2, and the rate of its intake therefore measures the rate of assimilation. The measurement of assimilation from the intake of CO_2 necessitates a complicated chemical analysis, which is therefore a very prolonged and laborious process. It is neither a very sensitive nor a highly accurate method. The following automatic method was therefore devised for recording normal rate of photosynthesis and for quickly indicating any change induced in that rate.

Automatic Recorder of Assimilation

Water-plants obtain their carbon from the carbonic acid dissolved in the water. When sunlight falls on these plants, carbonic acid gas is broken up, the carbon becomes fixed in the form of carbohydrates, and oxygen is evolved which rises as a stream of bubbles from the plant. The rate of evolution of oxygen thus measures the rate of assimilation.

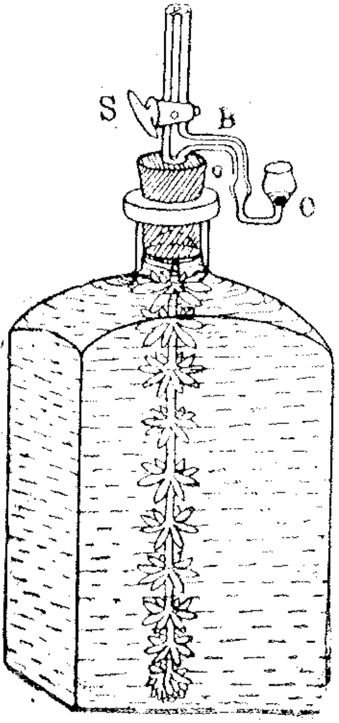

Fig. 103. The Plant-Vessel and the Bubbler.

S, stop-cock; B, Bubbler; O, mercury valve.

Numerous difficulties were encountered in making this method practical; they have been completely removed by the Automatic Recorder. A piece of water plant, *e.g.*, *Hydrilla verticillata*, is placed in a bottle completely filled with tank-water containing sufficient CO_2 in solution, the open end of which is closed by a special Bubbler apparatus, for measuring the oxygen evolved. The Bubbler consists of a U-tube, the further end of which is closed by a drop of mercury acting as a valve. The oxygen evolved by the plant, entering the U-tube, produces an increasing pressure, which eventually lifts the mercury valve and allows the escape of a bubble of the gas. The valve then immediately closes until it is lifted once more for escape of another equal volume of gas (fig. 103). The movement of the mercury completes an electric circuit, which either rings a bell or makes an electro-magnetic writer inscribe successive dots on a revolving drum (fig. 104). The automatic method eliminates all personal errors of observation; it is so extremely sensitive that it is possible to indirectly measure by its means, a deposit of carbohydrate as minute as a millionth of a gram.

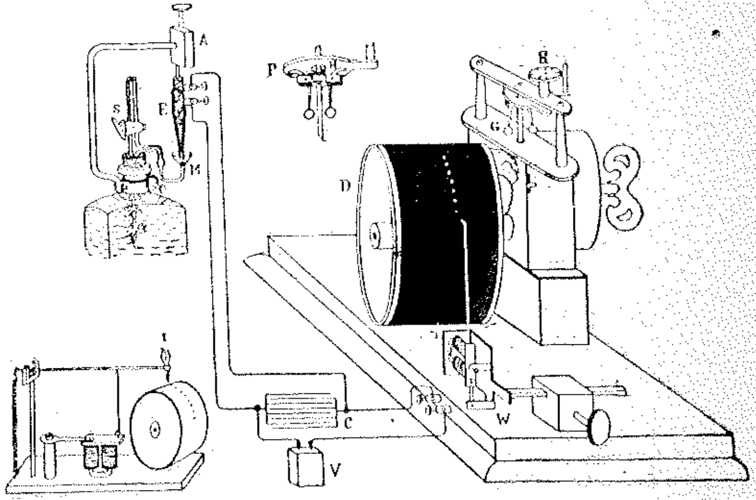

Fig. 104. The Automatic Recorder for Photosynthesis.

S, bubbler with stop-cock; E, the electric pencil for completing electric contact through drop of mercury, M; A, adjusting screw; V, voltaic cell; C, condenser; D, revolving drum; W, electro-magnetic writer; G, governor, shown separately at P with pair of hinged levers, H; I, ink-recorder. Electric bell not shown.

The following example illustrates the practical working of the apparatus. The plant with the apparatus is so placed as to face the northern light; the bell rings each time it has absorbed a certain amount of CO_2. If a person now stands obstructing the light, the assimilation is slowed down and the bell now strikes at longer intervals. When strong sunlight is thrown on the plant, the successive strokes on the bell become greatly quickened. The plant is such a sensitive detector of light that it may be employed as a photometer for indicating the slightest variations in the intensity of skylight.

The Hourly Variation of Assimilation

For this determination I took successive records from 7-30 a.m. until 5 p.m. for five minutes at a time. When the sun rose at 6-45 a.m. the light was too feeble to be effective. At 7-30 a.m. assimilation began, and the plant evolved four bubbles of oxygen in the course of five minutes; with the progress of the day it became more and more active until at 1 p.m., the activity increased four times that in the morning. The real reason for increased assimilation at 1 p.m. is the favourable condition of light and temperature. The activity declined in the afternoon and became arrested with the onset of darkness (fig. 105).

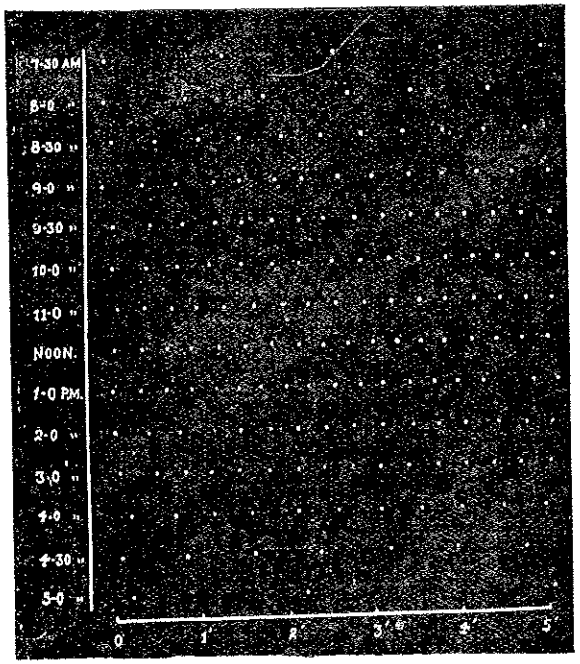

Fig. 105. Automatic Records of successive Bubblings for five minutes during different periods of the day.

Note the slow rate at 7-30 a.m. and 4-30 p.m., and the quick rate at mid-day.

Effect of Infinitesimal Trace of Chemical Substance

One of the most unexpected results, was the discovery of the extraordinary increase in the power of assimilation by inconceivably small traces of certain chemical substances. It was found that when these were diluted, one part in a billion, they produced an increase in the power of assimilation of more than a hundred per cent. The immediate and concrete demonstration of minute traces of chemicals on assimilation is of special interest, since it enables us to understand the effects of infinitesimal quantities of vitamin on general assimilation and of hormones on physiological reaction.

Formaldehyde, which in large doses acts as a poison, is found in a solution of one part in a billion, to produce an increase of activity of 80 per cent. The stimulating effect of traces of formaldehyde has a special significance in regard to the 'first product' of photosynthesis. There is reason to believe that this first product is formaldehyde, which by polymerisation, becomes converted into carbohydrate. The poisonous nature of formaldehyde stood in the way of acceptance of this view, but the experiment just described shows that traces of this substance, instead of being poisonous, actually enhance the photosynthetic activity.

Efficiency of the Photosynthetic Organ in Storage of Solar *Energy*

The results hitherto obtained indicate, in general, a very low order of efficiency in storage of energy. The methods employed have been defective from absence of means of exact measurement of the incident energy, from the indeterminate loss of the energy received and from the difficulty in the exact determination of the energy stored. The efficiency is found from the ratio of the energy stored Es, to the energy absorbed Ea.

$$\text{Efficiency} = \frac{\text{Es}}{\text{Ea}}$$

I have been successful in obviating the various difficulties in the accurate determination of the energy absorbed, and of the energy stored. The energy absorbed is found by two different methods, the Calorimetric and the Radiometric, these two independent determinations following each other in quick succession. While the energy absorbed is being determined, simultaneous measurement is made of the energy stored by the production of carbohydrate. This is calculated from the volume of oxygen evolved.

The efficiency of the photosynthetic organ is found to be much higher than had been usually supposed, being half that of an ordinary steam engine. In vigorous *Hydrilla* plant it is as high as 7·4 per cent.

The automatic method of record that has been described, can also be utilised in physico-chemical investigations, such as the determination of the rate of evolution of a gas under controlled conditions of temperature, of concentration, of intensity of light, of catalytic agents and others, either separately or in combination. It is obvious how it can be applied in various

ways for measuring chemical reactivity or velocity of chemical reactions, *e.g.*, as in the study of Vant Hoff's Law, of the effect of light on chemical change and of other allied phenomena.

(*Physiology of Photosynthesis*, 1925.)

XXV

THE SELF-RECORDING RADIOGRAPH

A diurnal periodicity is generally exhibited in the various activities of the plant and in the movements of its different organs. This periodicity must be related to external variations, notably of temperature and light. It would be impossible to analyse the resulting phenomenon unless a continuous record of changes in the intensity of light is secured with the same exactitude as that of variation of temperature. As regards these two principal factors, the effect induced by the rise of temperature is often antagonistic to that of increasing intensity of light. A rise of temperature, for example, enhances the rate of growth up to an optimum; light, on the other hand, acts as a stimulus in retardation of growth.

For full analysis of diurnal periodicity in plants, it thus becomes necessary to devise means for continuous record of variation of temperature and the changing intensity of light. In regard to the variation of temperature, a simple and reliable type of thermograph has been devised, by which it is easy to obtain a continuous record of the variation of temperature throughout the day and night. No apparatus is, however, available for the continuous registration of variation of the intensity of light.

The Selenium Cell

Selenium is well known for the characteristic diminution of its electric resistance under illumination.

When an electric current is maintained in the circuit, exposure of the selenium cell to light causes an increase of the galvanometer deflection. Several difficulties are, however, encountered in employing it for a continuous record of fluctuation of light for the whole day. The resistance of selenium undergoes a change under the polarising action of an electric current, the variation increasing with the strength and the duration of the current. The effect of polarisation is however negligible, if the current be feeble and of short duration. There is a possibility of another difficulty arising from the effect of daily variation of temperature on the normal resistance of the selenium cell. Allowance for this could be made by taking a continuous record of the effect of hourly variation of temperature on the resistance of the cell kept in darkness. Finally means have to be devised for automatic record of galvanometer deflections under changing intensities of light.

The Radiograph

The difficulties encountered in obtaining automatic record have been removed by the following devices :—

(*a*) The Wheatstone Bridge for balancing electric resistance of the selenium cell in dark and its upset on exposure to light.

(*b*) The arrangement of three electric keys which are automatically put on and off in regular sequence and at pre-determined intervals.

(*c*) The Self-recording Galvanograph.

The Wheatstone Bridge

This is diagrammatically represented in B (fig. 106). The resistance of the particular selenium cell S is 76,000 ohms in the dark. An approximately equal resistance is placed in the second arm of the bridge. A rheostat having a large number of turns of fine wire with a sliding contact is used for the two variable arms of the bridge, diagrammatically represented by a straight line. Under exact balance the galvanometer deflection is reduced to zero. The balance is upset when the selenium cell is exposed to light and the resulting deflection gives a measure of the intensity of light.

The Automatic Keys

After previous adjustment of the balance in the dark the electric circuit is completed by the closure of key K_1; the selenium cell is next exposed to light by an automatic electro-magnetic shutter T. The deflection of the galvanometer is recorded by means of electric sparks on a piece of moving paper. The different operations are carried out in proper sequence by the automatic devices described below.

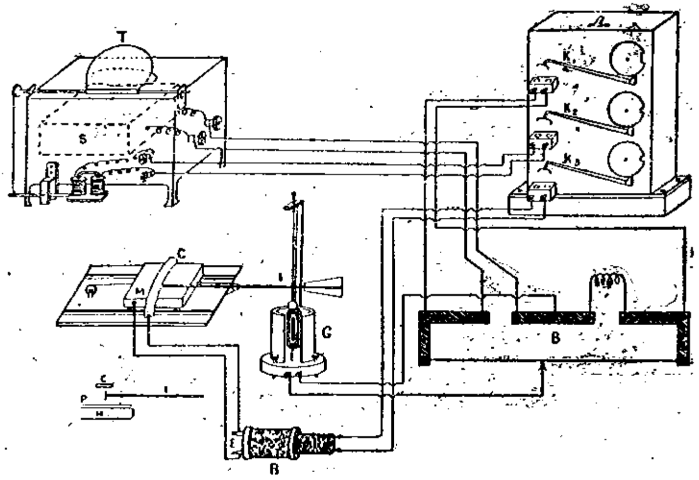

Fig. 106. The Self-recording Radiograph.

The selenium cell, S is periodically exposed to light by the electromagnetic shutter, T. The selenium cell forms one arm of the Wheatstone Bridge, B. The three keys, K_1, K_2, K_3, are periodically closed and opened by clockwork. G, the recording galvanometer with index, I, carrying double-pointed platinum at its end, which moves between the metal strip, C, and the plate, M. R, sparking coil with its electrodes connected with C and M. The battery is not shown in the figure (see text).

K_1 completes the battery circuit for about 10 seconds, by which time the record is completed. The successive records for variation of light are taken at intervals of 15 minutes; the periodic closures of the circuit are thus for 10 seconds at intervals of 15 minutes. This short passage of the current is found in practice to cause no polarisation.

The second key K_2 actuates an electromagnetic device by which the trap-door, T, is opened for the definite period of one second; the selenium cell S inside the dark box is thus exposed to light for this length of time. The trap-door is seen in the diagram immediately above the dark box. In reality it is at the upper end of a vertical tube the inside of which is coated with lamp-black to prevent side reflection. The light that falls on the selenium cell is thus from a definite area of the sky. The intensity of light from the sky at different periods of the day causes deflection of the galvanometer which is proportional to that intensity. The maximum deflection of the galvanometer employed is attained in the course of 3 seconds after the exposure.

The third key K_3 is for completion of spark circuit R for record of the maximum galvanometric deflection, three seconds after the exposure of the selenium cell. This key actuates a sparking coil R, the vibrating interrupter of which is not shown in the figure. The spark, thus produced, punctures the maximum deflected position of the galvanometer index on a moving piece of paper attached to the plate M.

The successive closure and opening of the keys are made automatically and in proper sequence by means of a clock work, the whole process being repeated at intervals of 15 minutes.

The Galvanograph

The most difficult problem is the automatic record of galvanometric deflections. This can be secured without any difficulty by means of photography. A spot of light reflected from the galvanometer mirror is in this case allowed to fall on a photographic plate which descends at an uniform rate by clockwork. This, however, entails the use of a dark room and subsequent development of the plate. The trouble was avoided by the device of direct record of the galvanometer deflection by means of electric sparks.

The sparking method has been previously employed in which the deflected index of the galvanometer in connection with one electrode of an induction coil leaves a spark record on a moving piece of paper. Several difficulties are, however, encountered in employing this method for record with a highly sensitive galvanometer. There is a liability of leakage of the high tension current into the galvanometer circuit. The discharge of the spark gives moreover a backward kick to the index by which the normal deflection undergoes an unknown variation.

The above difficulties have been removed in the following manner. The moving coil of the sensitive D'Arsonval galvanometer, has a long glass index I, at right angles to the plane of the coil. The glass index is

coated with shellac varnish to render it highly insulating. The index is projected to a short distance on the opposite side, for attachment of a counterpoise; this takes the form of a vertical vane of mica which acts as a damper. The galvanometer itself is of an aperiodic type, and the addition of the damper makes it perfectly dead-beat. The sensitiveness of the galvanometer is such that a micro-ampere of current produces a deflection of 10 mm. of the index. The recording index has attached to it a short vertical piece of thin platinum wire pointed at its two ends; this end of the index moves between a sheet of metal M, on which is spread the recording paper, and a semi-circular piece of narrow metal sheet C. The metal sheet M is mounted on wheels and moves at an uniform rate by clockwork. Record is made by sparks. One electrode of the sparking coil is in connection with C, and the other with M. The sparking thus takes place simultaneously, above and below the vertical and double-pointed platinum wire carried at the end of the index. There is thus no resultant kick, and the index remains undisturbed. The sparking, as previously stated, takes place three seconds after exposure of the selenium cell to light, by which time the deflection reaches its maximum. The record thus consists of successive dots at intervals of 15 minutes, the dots representing the maximum deflections of the galvanometer corresponding to the intensities of light.

The record given in figure 107 was taken about the end of January; the sun rose at about 6-45 a.m. and set at 5-30 p.m. The twilight is very short in the tropics; the sky is feebly lighted about 6 a.m.; it becomes dark about 6 p.m. The record shows the intensity of light to be exceedingly feeble at 6 a.m. The rise in the intensity was rapid, attaining the maximum at 12 noon.

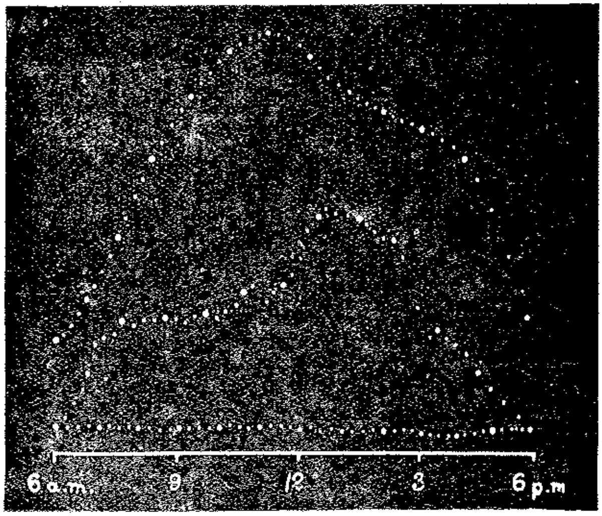

Fig. 107. Radiograph of variation of intensity of light from the sky during 12 hours in winter. The upper record shows the variation on a bright day, the maximum intensity being attained at 12 noon. The lower record exhibits irregular variation on a cloudy day. The practically horizontal record above the base line shows that the electric resistance of selenium cell is practically unaffected by variation of temperature. Successive thin dots at 15 minutes' interval, thick dots at intervals of an hour.

This will be designated as the light-noon. The intensity of light then declined at a rate slower than the rise; after 5 p.m. the fall of intensity was extremely rapid.

It was stated that there was a possibility of change of resistance induced by diurnal variation of temperature. In order to determine the extent of this variation, a spark record was also obtained before exposure to light. The dotted record near the base (fig. 107) shows that the resistance remained practically constant, inspite of the variation of the temperature.

An important point arises as regards the diurnal variation of light and of temperature, and determination of their periods of maximum and minimum. For this purpose records of diurnal variations of temperature and of light were taken on the same day in summer with the thermograph and the radiograph. The two curves are given in figure 108; it will be seen that while the maximum intensity of light is at 12 noon, the thermal maximum is at about 2 p.m. The thermal noon is thus two hours later than the light-noon. Light disappears at night from 6 p.m. to 6 a.m., that is to say, the period of minimum or zero light is prolonged for 12 hours. But the fall of temperature is gradual, and the minimum is attained at about 5 a.m. which is the thermal dawn. The characteristic variations of these two important factors should be borne in mind, since the diurnal movements of plants are modified by the

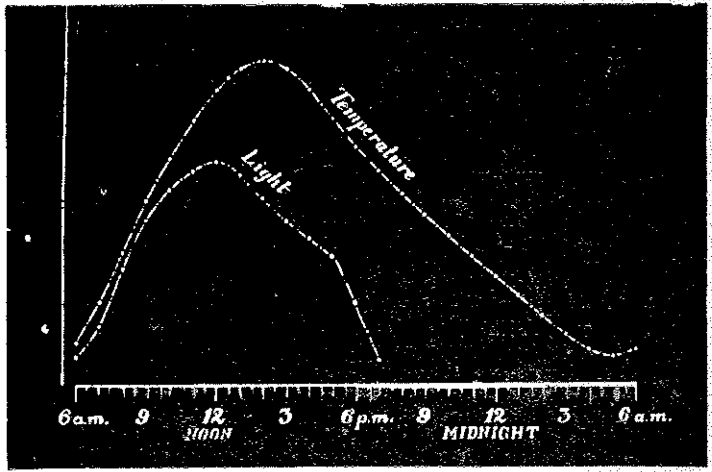

Fig. 108. Record of diurnal variations of light and of temperature in summer.

algebraical summation of the effects of light and of temperature.

It is sometimes desirable to carry out researches during a period when the intensity of light remains approximately constant. This period is found to be between 11 a.m. and 1 p.m. for the variation is then only ±5 per cent. of the mean.

The record given of the diurnal variation of light is true of days when the sky is clear. But the passage of clouds causes change in the intensity which is accurately recorded by the Radiograph. A record of such irregular variation in a stormy day is given in the lower record of figure 107.

(*Life Movements in Plants, Vol. IV*, 1923.)

XXVI

THE HIGH MAGNIFICATION CRESCOGRAPH

The difficulty of investigations on growth arises from its extreme slowness, which is two thousand times slower than the movement of the snail. The 'auxanometers' usually employed magnifies growth to about 20 times; under this magnification several hours must elapse before growth becomes perceptible. During this long period the external conditions, such as light and warmth, undergo change thereby confusing and vitiating the result. The external conditions can be kept constant for a few minutes only; hence the effect of variation of an individual factor can only be found by increasing the magnification to about ten thousand times and thus reducing the period of the experiment. The apparatus devised for this purpose not only produces this enormous magnification but also automatically records the rate of growth and its induced variation in the course of time as short as a minute or so.

The recorder consists of a compound system of two levers; the first magnifies a hundred times, and the second enlarges the first a hundred-fold, the total magnification being thus ten thousand times. The difficulty introduced by the weight of levers was surmounted by the employment of navaldum, an alloy of aluminium, which combines great rigidity with exceptional lightness. The friction at the points of support was removed by the employment of jewel bearings. The record is taken on a smoked glass plate kept oscillating to and from by means of a crank K and eccentric R, actuated by a clockwork C (fig. 109). Successive dots are produced at definite intervals which could be made to vary from 1 to 10 seconds.

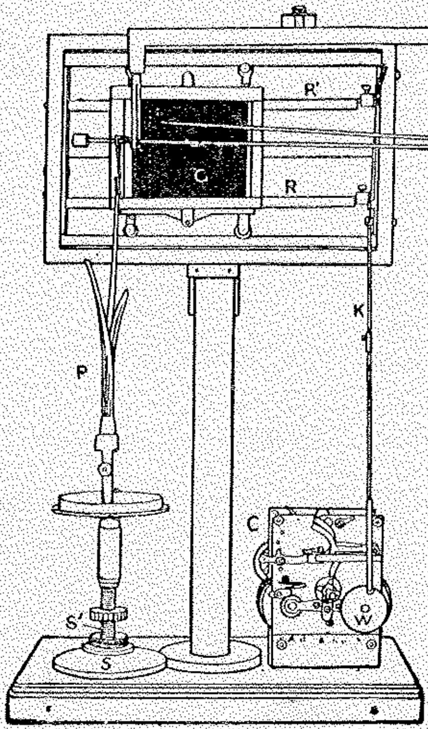

Fig. 109. The High Magnification Crescograph.

P, plant; C, clockwork for periodic oscillation of recording smoked glass plate G; S S', micrometer screws; K, crank; R, eccentric; W, rotating wheel.

Two different methods are employed for obtaining the record. In the first, the records are taken on a stationary plate, the first series under normal condition, and the second under a given variation. The increase or diminution of intervals between successive dots in the two series, demonstrates the stimulating or depressing nature of the changed condition.

In the second method, the record is taken on a plate moved at a uniform rate by clockwork. A curve is thus obtained, the ordinate representing growth-elongation and the abscissa, the time. The increment of length divided by the increment of time gives the rate of growth at any part of the curve. As long as growth is uniform, so long the slope of the curve remains constant. Enhancement of the rate of growth by a stimulating agent causes an upward flexure of the curve; a depressing agent, on the other hand, lessens the slope of the curve.

Determination of the Absolute Rate of Growth

The record of growth was taken with a vigorous specimen of *S. Kysoor* on a stationary plate.

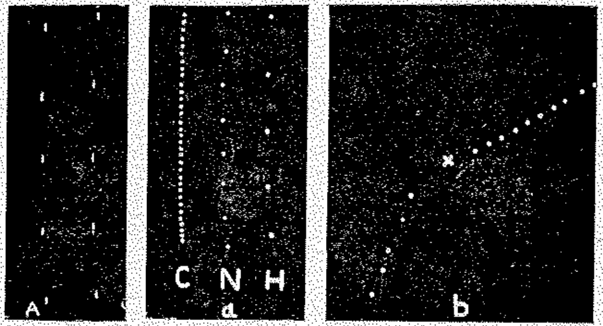

Fig. 110. Crescographic Records.

(A) Successive records of growth at intervals of one second (magnification 10,000 times). (*a*) Effect of temperature taken on a stationary plate; N, normal rate of growth; C, retarded rate under cold; H, enhanced rate under warmth; (*b*) record on moving plate, where diminished slope of curve denotes retarded rate under cold. (Magnification 2,000 times.)

For securing uniformity of growth, it is advisable that the plant be kept in darkness or uniform diffused light.

So sensitive is the recorder that it shows a change of growth-rate due to slight increase of illumination by the opening of an additional window. The oscillation frequency of the recording plate was once in a second, the magnification being 10,000 times. After taking the first series of record, the second series was obtained after an interval of 15 minutes (fig. 110A) The magnified growth elongation is 9·5 mm. per second; since it is quite easy to measure 0·5 mm., it is possible to record growth for a period as short as 1/20th of a second. It is further seen that the Crescograph enables us to magnify and record a length of 0·0005 mm. which is a fraction of a single wave length of light.

Employing one second, as the unit of time and μ or micron as the unit of length (1/1000 mm.), the absolute rate of growth of *S. Kysoor* is found as follows :—

If m be the magnifying power, l the average distance between successive dots in mm. at intervals of t seconds,

$$\text{the rate of growth} = \frac{l}{mt} \times 10^3 \text{ per second}$$
$$= \frac{9 \cdot 5}{10{,}000} \times 10^3 \text{ per second.}$$
$$= 0 \cdot 95 \ \mu \text{ per second.}$$

Effect of Variation of Temperature.

The effect of variation of temperature on growth is shown in fig. 110*a*. The middle series N was taken at the temperature of the room; the next C was obtained when the temperature was lowered by a few degrees. Finally H was taken when the plant chamber was warmed. The spaces between successive dots are shortened under cooling which induces a diminished rate of growth. The enhancement of the rate of growth by rise of temperature is exhibited by the widening of intervals between successive dots. The effect of lowering of temperature in retardation of growth is also exhibited by record (fig. 110*b*) taken on a moving plate, in which the diminished slope of the curve demonstrates the depressed rate of growth.

Effect of Chemical Agents

The effects of manures, anæsthetics, drugs and poisons, can be similarly determined in the course of a few minutes, and with unprecedented accuracy. A few agents only have hitherto been employed in stimulating growth, whereas there are numerous others of whose actions we have been profoundly ignorant. The crude method hitherto employed in the application of a few chemical agents and of electricity has not been uniformly successful. The cause of the anomaly is found in the discovery of an important factor, namely, the dose of application, which has hitherto not been taken into account. It was thus found that while a particular intensity of electrical current accelerated growth, any excess above a critical point retarded it. The same is true of chemical stimulants; a striking result was obtained with certain poisons which in normal doses killed the plant, but in doses sufficiently minute acted as a highly efficient stimulant in promotion of growth.

The Balanced Crescograph

The growth of plants is affected by changes of environment which are even below human perception. It now became necessary to devise a new method of still greater sensitiveness which would instantly show by the up- or down-movement of an indicator, the stimulating or depressing nature of an agent on growth. The desideratum is to compensate the up-movement of growth by some regulating device, by which the plant is made to descend exactly at the same rate at which the growing tip of the plant was rising, whatever that rate may be. The special difficulty encountered was in obtaining exact balance for widely varying rates of growth in different plants, and even in the same plant under different conditions. In the Balanced Crescograph, (fig. 111) a train of revolving clockwork actuated by the fall of a weight, lowers the plant at the same rate at which it is growing. The exact adjustment is obtained by the gradual turning of a screw to the right or to the left, by which the rate of compensating fall is retarded or accelerated. In this way the rate of growth becomes exactly compensated, and the recorder now dots a horizontal line instead of the former curve of ascent. The turning of the adjusting screw of the Balanced Crescograph also moves an index against a circular scale (not shown in the figure) so graduated that its reading at once gives the rate at which the plant is growing at that instant. When balanced, the recording apparatus is extraordinarily sensitive. Any change, however slight, in the environment is at once indicated by the upset of the balance with up- or down-movement of the curve. This method is so extremely sensitive that it is possible to detect variation of rate of growth so excessively minute as 1/1500 millionth of an inch per second.

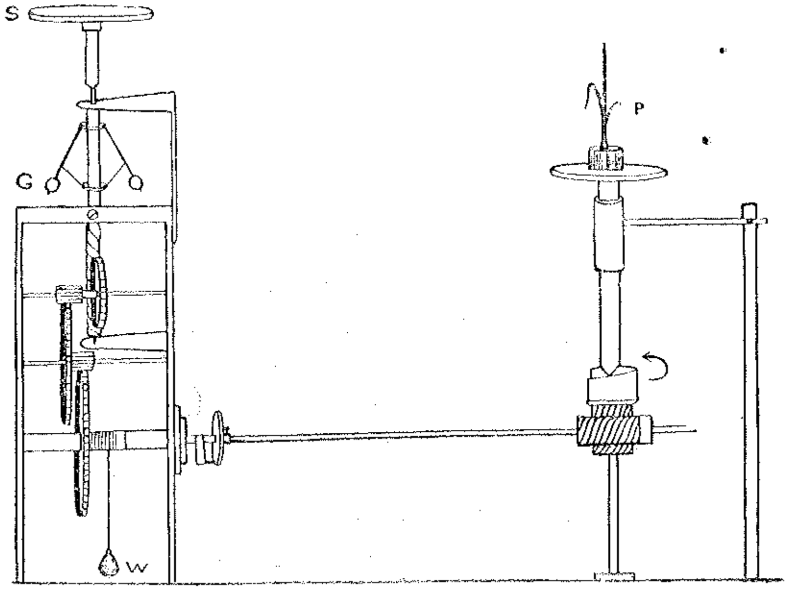

Fig. 111. The Balanced Crescograph.

Compensation of growth-movement produced by equal subsidence of the holder containing the plant (P). Adjusting screw (S) regulates the speed of the governor (G). W, heavy weight actuating clockwork.

As an illustration of the delicacy of this method, a

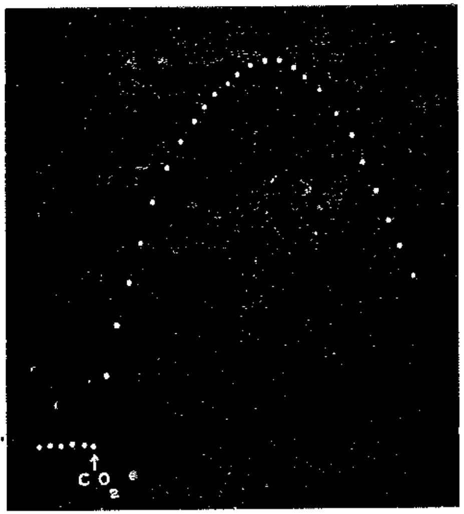

Fig. 112. Record showing the effect of carbonic acid gas on growth. Horizontal line at the beginning indicates balanced growth. Application of carbonic acid gas induces enhancement of growth, shown here by up-curve, followed by depression, exhibited by down-curve. Successive dots at intervals of ten seconds.

record is given of the effect of carbonic acid gas on growth (fig. 112). A jar is filled with this gas, and emptied over the plant; the invisible gas, on account of its heavier weight, falls in a stream and surrounds the plant. The record shows that this gave rise to an immediate acceleration of growth, which continued for two and-a-half minutes; this preliminary acceleration was followed by retardation of growth as shown by the down curve. The Balanced Crescograph thus not only exhibits the beneficial effect of an agent, but also indicates the dose which prolongs the beneficial effect.

Effect of Wireless Stimulation on Growth

Growth is modified by the action of visible light; two different effects are produced depending on the intensity. Strong stimulus of light induces a diminution while feeble stimulus induces an acceleration of the rate of growth. The effectiveness of light in modifying growth depends moreover on the quality of light; the effect is very strong in the ultra-violet region of the spectrum with its extremely short wave-length of light; it declines almost to zero as we move towards the less refrangible rays, the yellow and the red, with their comparatively long wave-length. As we proceed further to the infra-red region we come across the vast range of electric radiation, the wave-lengths of which vary from the shortest wave I have been able to produce (0·6 cm.) to others which may be miles in length. There thus arises the important question whether plants perceive and respond to the long ether-waves, including those employed in signalling through space.

At first sight this would appear to be very unlikely, for the most effective rays are in the ultra-violet region with wave-length as short as 20×10^{-6} cm.; but electric waves used in wireless signalling are 50,000,000 times as long. The perceptive power of our retina is confined within the very narrow range of a single octave, the wave-lengths of which lie between 70×10^{-6} cm. and 35×10^{-6} cm. It is difficult to imagine that plants could perceive radiations so widely separated from each other as the visible light and the invisible electric waves.

The results obtained prove, however, that electric waves are effective in modifying the rate of growth. The experiment was carried out with the help of a portable electric Radiator, the intensity of radiation being capable of variation. The Radiator was placed at a distance of 200 metres from the growing plant which was suitably mounted on the Balanced Crescograph.

Effect of feeble Stimulation.—The response was found to be an acceleration of growth as seen in fig. 113 (*a*). This is analogous to the stimulating action of light of sub-minimal intensity.

Effect of strong Stimulation.—Even more striking is the effect of stronger stimulation; the balance was immediately upset, indicating a retardation of the rate of growth (fig. 113 *b*). The latent period, *i.e.*, the interval between the incident wave and the response, was only a few seconds. The record given in the figure was obtained with the moderate magnification of 2,000 times.

Under an intensity of stimulus slightly above the sub-minimal, the response exhibited retardation of growth followed by quick recovery, as seen in the series of records given in figure 113 (*c*). The perceptive range of the plant is inconceivably greater than ours; it not only perceives, but also responds to different rays of the vast ethereal spectrum.

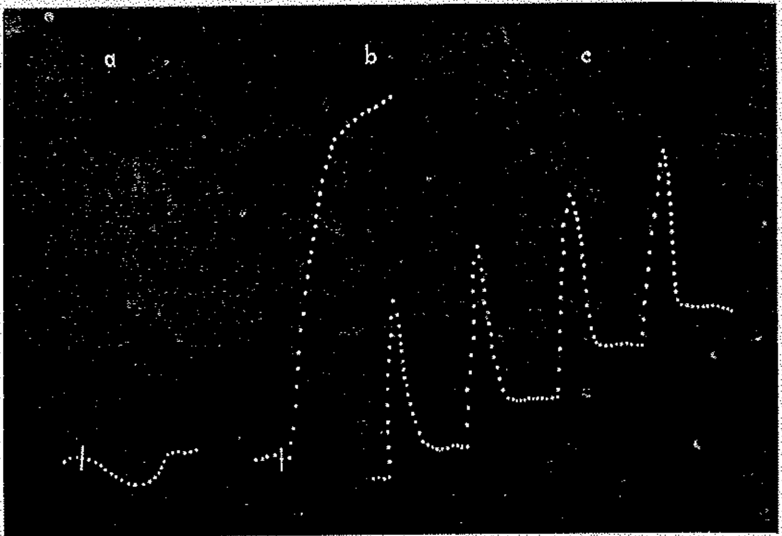

Fig. 113. Record of responses of plant to wireless stimulation. (*a*) Response to feeble stimulus by acceleration of growth; (*b*) response to strong stimulus by retardation of growth; (c) response to medium stimulation—retardation followed by recovery. Down-curve represents acceleration, and up-curve retardation of growth (seedling of wheat).

(*Proc. Roy. Soc. Oct.* 1917 *and Transactions Bose Institute*, 1919.)

XXVII

THE MAGNETIC CRESCOGRAPH AND THE MAGNETIC RADIOMETER

In winter the growth appears to be in a state of arrest; in reality growth may persist but its rate is too slow to be detected even by the High Magnification Crescograph in which two levers produce a compound magnification of 10,000 times. It may be thought that further magnification could be obtained by a compound system of three levers; there is, however, a limit to the number of levers that may be employed with any advantage, for the slight overweight of the last lever becomes multiplied, exerting a tension so great on the plant as to interfere with the normal rate of its growth. The friction at the bearings also becomes added up by an increase in the number of levers which obstruct the free movement of the last recording lever. Magnification requiring additional material contact between different levers have, therefore, to be abandoned and it became necessary to devise an ideal method of magnification without contact. In the device perfected for this purpose a single magnifying lever attached to a growing plant upsets a very delicately balanced magnetic system (cf. fig. 114). The indicator is the reflected spot of light from a mirror carried by the deflected magnet. I have thus been able to produce a magnification as high as 50 million times. This order of magnification would lengthen a single wave of sodium light to 2,500 cm. It is obvious that this method of super-magnification would be of great help in many physical investigations.

The Demonstration Crescograph

Such an enormous magnification can not be employed in ordinary investigations on growth, for the indicating spot of light rushes on like a flash. I had, therefore, to reduce the magnification to a million times by which demonstrations of a striking character on various phenomena of growth can be given before a large audience. The following may be taken as a typical example :—

The normal rate of growth of the experimental flower-bud of *Crinum Lily* was 0·0006 mm. per second. A scale 3 metres long divided into centimetres was placed against the screen. A metronome beating half seconds is started at the moment when the spot of light transits across the zero division ; the number of beats is counted till the index traverses 300 cm. At the normal temperature of the room (30° C.) the index traversed 300 cm. in 5 seconds. As it is easy to measure 1 mm. on the scale, the Magnetic Crescograph enables measurement of growth in a period shorter than 1/500th of a second.

After observing the normal rate at the temperature of the room, the plant chamber was cooled to 26° C. by blowing in cooled water vapour ; the time now taken by the spot of light to traverse the scale was 20 seconds, *i.e.*, the growth-rate was depressed to one-fourth. Under continuous lowering of temperature there was a continuous retardation, till at 21° C. growth was arrested. Warm vapour was next introduced raising the temperature of the plant-chamber to 35° C. The spot of light now rushed across the whole length of the scale in $1\frac{1}{2}$ seconds, growth being enhanced to more than three times the normal rate. The entire series of experiments on the effect of variation of temperature on growth was completed in the course of 15 minutes.

Experimental demonstrations of the action of light, and of various chemical agents can also be given in a similar manner.

The Magnetic Radiometer

As an example of the application of the method of high magnification in physical investigations, I describe the Magnetic Radiometer in determination of the energy of different rays of the solar spectrum by measuring the elongation of a metallic wire coated with lamp-black. The particular spectral ray falling on the wire is absorbed, and thus raises the temperature proportionately to the energy of radiation. The resulting increase of length is so minute as to be undetectable by any method of magnification hitherto available.

A diagrammatic representation of the apparatus is given in fig. 114. W is a length of zinc wire which becomes lengthened by rise of temperature produced by absorbed radiation. It is attached by a hook to the short arm of a long magnetic lever, the N end of which is lowered by any elongation of the sensitive wire. In front of the N end of the magnetic lever is suspended a small magnetic needle with an attached mirror. As the N pole of the magnetic lever is lowered, it produces an increasing deflection of the suspended needle, which is magnified by the spot of light reflected from the attached mirror. The sensitiveness of the apparatus is very greatly enhanced by the employment of a perfect system of astatic needles.

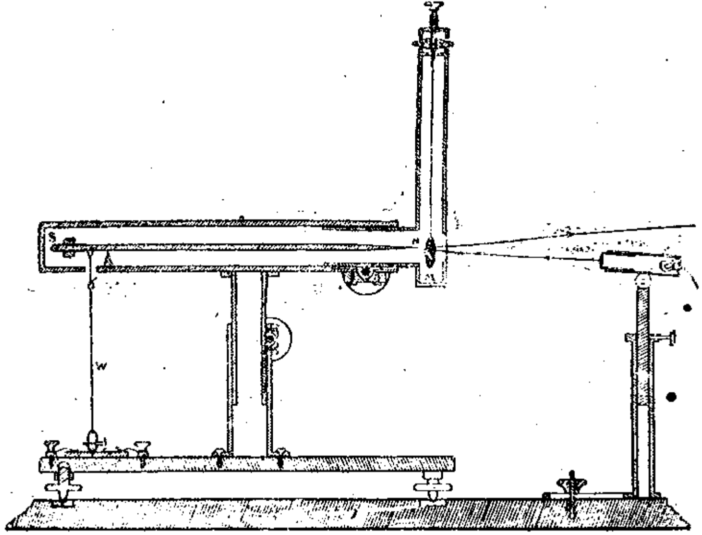

Fig. 114. The Magnetic Radiometer.

SN, magnetic rod supported on fulcrum; short arm of magnet attached to sensitive strip of metal W. Elongation of strip lowers the N end, which causes deflection of the suspended needle with attached mirror M. Deflection magnified by reflected spot of light.

This method for the measurement of radiation is extraordinarily sensitive. For instance, there is an apparatus permanently adjusted in the Institute in which the sensitive element is a thin strip of ebonite which is enclosed in a tube with a narrow slit in front. When any person walks at some distance past the instrument, the indicating spot of light remains perfectly quiescent until the individual is in line of sight of the sensitive strip; a sudden deflection is then produced by the radiation which is emitted from the human body, through thick warm clothing and a heavy overcoat; when the person walks past the line of sight the indicating spot of light returns to its original zero.

The zinc wire was surrounded by a wooden tube with a narrow slit for the passage of the spectral rays. The slit was open through a length of 10 cm., the brass piece to which the strip was soldered being protected from radiation. A very thin piece of mica covered the slit, to prevent air-currents getting access to the narrow chamber in which the sensitive strip was enclosed. The exceedingly thin piece of mica was found practically to have no effect in obstructing radiation. The whole apparatus was placed inside a larger wooden box covered with non-conducting felt. A round hole in front of the box (covered with a piece of thin glass) allowed the passage of the spot of light reflected from the mirror attached to the suspended magnetic needle.

It is necessary to give a detailed account of precautions to be observed, because the instrument is so sensitive that it detects the slightest difference in the temperature of the different portions of the same mass of air. Gases are highly non-conducting, and their temperature hardly attains a perfect uniformity. In these circumstances it is best to take precautions against contact of the strip with the outside air, which, again, should not be disturbed in any way. The observer never moves from his place in the dark room, which is closed on all sides.

The spectrum produced by the carbon disulphide prism was found to extend beyond the limit of the visible red, this extension into the infra-red region being almost 6 cm., or about one-third the breadth of the visible spectrum.

The extreme sensitiveness of the Radiometer was also exhibited by its discrimination of the radiation components of the morning and midday light. In the morning the intensity of the blue rays in the spectrum was found to be slightly less than at midday. This is due to the greater scattering of the short waves by the thicker stratum of the atmosphere through which the light has to pass in the morning.

The energy of radiation in the different regions of the spectrum was compared on January 16 and 19, 1923. It should be remembered that the determination of the energy of the different rays was made upon the spectrum given by the carbon disulphide prism. The following results for the 16th and 19th January are seen to be practically the same.

Table showing the Distribution of Energy in the Spectrum produced by the CS_2 Prism

Wave-length.	Energy of radiation. 16th January.	Energy of radiation. 19th January.	Mean.
Infra-red 850 μμ (?)	90	80	85
Infra-red 790 μμ (?)	148	146	147
A 760 ,,	146	144	145
a 720 ,,	135	129	132
B 680 ,,	120	120	120
C 656 ,,	96	98	97
D 590 ,,	72	70	71
E 527 ,,	43	41	42
F 486 ,,	28	26	27
G 430 ,,	12	8	10

Radiation was detected at some considerable distance beyond the extreme red. At about 850 μμ the mean deflection of the Radiometer was found to be 85 divisions; at 790 μμ the energy was found to be 147, which was the maximum. At A (760 μμ) the deflection declined to 145; at *a* (720 μμ) it was reduced to 132; C (656 μμ) gave a deflection of 97. At the sodium line D (590 μμ) the reading was 71; the energy of the spectrum underwent a further and continuous decline; at E, F, and G the deflections were 42, 27, and 10 respectively.

(*Physiology of Photosynthesis*, 1925.)

XXVIII

THE RESONANT RECORDER

The exact determination of extremely short intervals of time is an important problem in various investigations. This is specially so in the measurement of time relations of different phases of response of living tissues.

When the sensitive pulvinus of *Mimosa pudica* is directly stimulated, say by an electric shock, a responsive contraction and fall of the leaf is initiated after the lapse of a short interval. After the completion of the fall of the leaf the contracted pulvinus slowly recovers as seen in the re-erection of the leaf. The lost time between the incidence of stimulus and the beginning of responsive movement is designated as the *Latent Period*. If instead of direct stimulation of the pulvinus, stimulus be applied on the petiole at a certain distance from the motile organ, then an excitatory impulse is transmitted through the intervening distance. The time-interval between stimulus and response will now be longer than under direct stimulation; the latent period of the pulvinus and the length of transmission afford sufficient data for the determination of the velocity of excitatory impulse in the plant, which I have shown elsewhere, is analogous to the nervous impulse in the animal.

The response of Mimosa is recorded by means of a writing lever suitably attached to the leaf (fig. 115).

The friction of the writing point against the smoked glass surface, however, introduces serious error in the accurate record of the amplitude and time-relations of the response-curve. The difficulty has been overcome by the writer being thrown into resonant vibration in consequence of which the record consists of a series of dots; the error arising from friction of continuous contact is thus completely avoided.

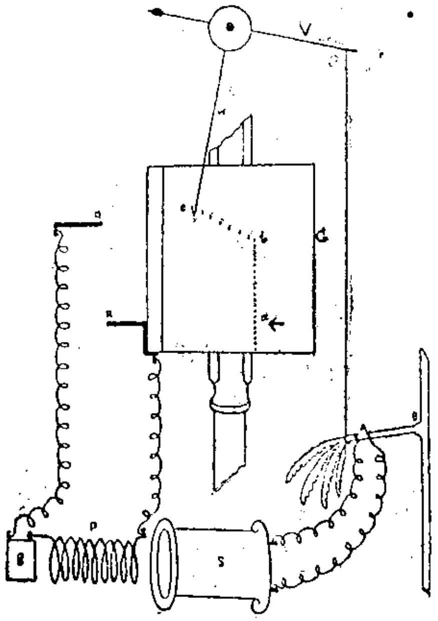

Fig. 115. Diagrammatic representation of the Recorder.

V, one arm of lever attached to leaf; W, the writer. The falling plate during descent makes electric contact of R with R′, causing induction-shock by the secondary coil S. Stimulus applied at *a* causes response later, at *b*.

The Resonant apparatus consists of the writer, made of fine steel wire tuned in different cases, to vibrate

10, 20, or 200 vibrations per second. The writer is suspended at the centre of a circular electromagnet, the current in which is periodically interrupted by the reed C (fig. 116). When the writer and the reed are exactly tuned then the vibration of the reed throws the writer into a sympathetic vibration.

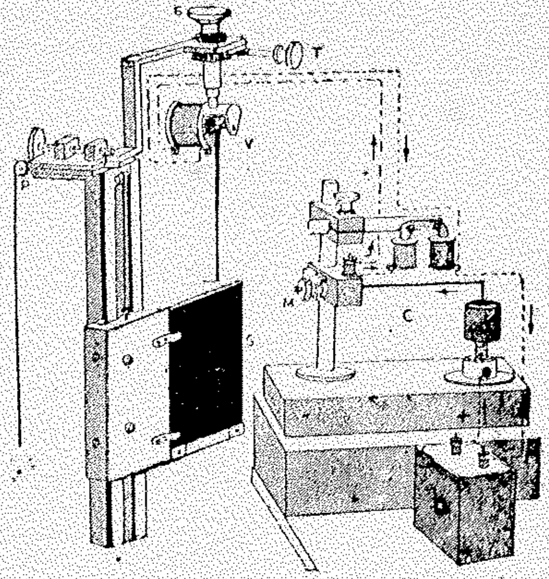

Fig. 116. Upper part of Resonant Recorder. (From a photograph.)

Thread from clock, not shown, passes over pulley P, letting down recording-plate; S, screw for vertical adjustment; T, tangent-screw for exact adjustment of plane of movement of recorder parallel to writing-surface; V, axis of writer supported perpendicularly at centre of circular end of magnet; C, the vibrating reed; G, smoked glass plate.

Determination of the Latent Period.

The reliability and accuracy of this method of automatic record of extremely short intervals of time is

shown in the following curve (fig. 117) which gives the latent period of the pulvinus of Mimosa. The writer

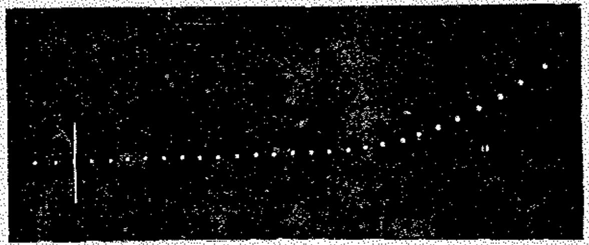

Fig. 117. Record of Latent Period of Mimosa with 200 Vibration Recorder.

was tuned to vibrate 200 times in a second, and the interval between successive dots therefore represents 1/200 of a second. It is not difficult to measure one-fifth of the distance between successive dots, and calculation can therefore be carried into thousandths of a second. In the present case there are 15·2 spaces between the stimulus and the initiation of response. The latent period of the specimen is therefore 0·076 of a second. The average value of the latent period of the pulvinus of Mimosa is found to be 0·1 second.

Determination of the Velocity of Impulse

The complete apparatus is shown in figure 118. An electrical shock was in the following experiment applied on the petiole at a distance of 30 mm. from the pulvinus, at the instant marked by the vertical line (fig. 119). The frequency of vibration of the writer was 10 per second. The interval between stimulation and the beginning of response is 16·2 spaces, or 1·62 seconds. A repetition of the experiment gave the same result. Stimulus was next applied directly on the pulvinus and the latent period was found to be about

0·12 seconds. The velocity of transmission of excitation in the particular specimen was thus found to be

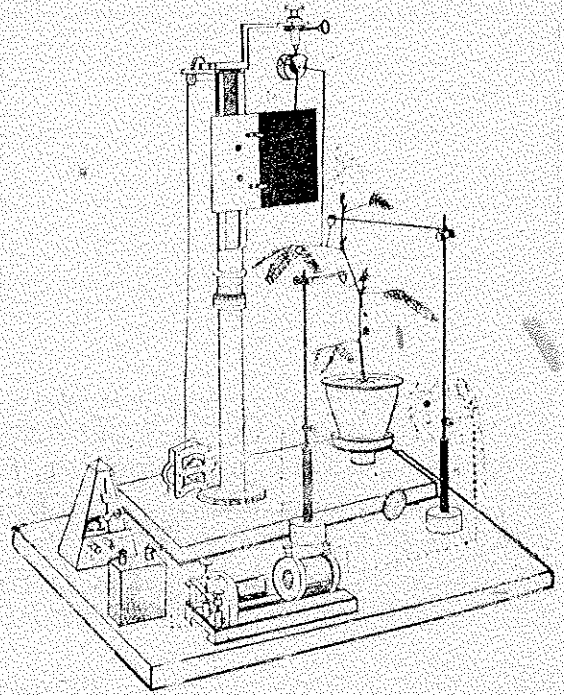

Fig. 118. Apparatus for determination of Latent Period and Velocity of Transmission of Excitation in *Mimosa*.

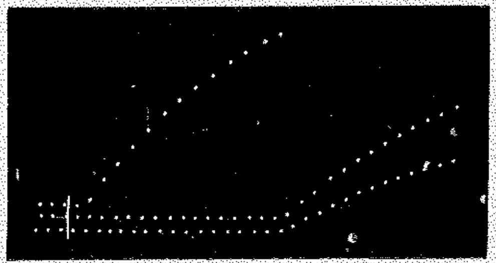

Fig. 119. Determination of velocity of Transmission of Excitation in petiole of Mimosa. Two lower records are in response to indirect stimulation applied at a distance of 30 mm.; upper record of response to direct stimulation gives the latent period. Recorder tuned to 10 V per second.

20 mm. per second. In thinner specimens the velocity is often found to be as high as 400 mm. per second. The velocity of impulse in Mimosa is slower than the nervous impulse in higher but quicker than that in lower animals.

The transmission of excitation is correspondingly modified by all conditions which modify the transmission of excitation in the animal nerve. The polar action of a constant electric current is identical in the two cases. In both Mimosa and animal nerve the velocity of transmission is increased within limits by a rise of temperature (fig. 120). In both, transmission can be arrested temporarily or permanently by various physiological blocks. The conducting power is temporarily arrested by a block produced by the passage of an electric current in a portion of the conducting tissue through which the impulse is being transmitted; this electrotonic block is removed on the stoppage of the current. Finally, poisonous solutions abolish the conducting power of both animal and plant. These results offer conclusive proof that the conduction in the plant is a phenomenon of propagation of protoplasmic excitation as in the nerve of the animal.

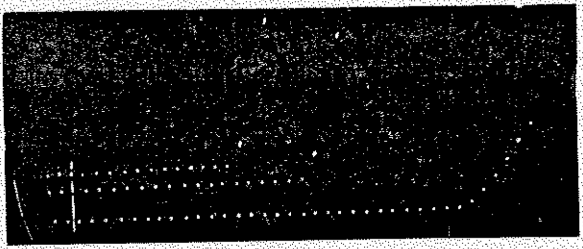

Fig. 120. Effect of Rise of Temperature in enhancing Velocity of Transmission. The three records from below upwards are for temperatures of 22° C., 28° C. and 31° C. respectively.

The characteristics of contractility and conductivity are thus shown to be exhibited not only by animal but also by plant tissues. In the animal the cardiac tissue exhibits automatic and rhythmic pulsations. In the plant a similar activity is manifested by the leaflet of *Desmodium gyrans*, the well known Telegraph plant.

The Resonant Cardiograph

The record of the pulsation of the animal heart by the Cardiograph labours under the unavoidable difficulty of continuous frictional contact introducing error in the correct record of the amplitude and time-relations of the heart-beat. The drawback of continuous contact has been removed in my Resonant Cardiograph which records the pulsation with great precision by means of periodic dots, the Cardiogram being also its own chronogram. The automatic method of registration of extremely short intervals of time can be utilised with great advantage for this and other investigations.

The Characteristics of Cardiac Pulsation.

The Resonant Cardiograph inscribes the different phases of the heart-beat with unprecedented accuracy. The systolic contraction and its persistence, the diastolic expansion and the subsequent pause, and any variation of these under external agencies, can thus be quantitatively determined. The cardiograms of different animals show, moreover, certain characteristic differences in regard to time-relations, as illustrated by records of tortoise, of frog and of Ophiocephalus fish given below.

The writing lever was tuned to vibrate 20 times in a second, the magnification produced being about 8 times. The time-relations, it is to be remembered, is found from the intervals of successive dots $\frac{1}{20}$ second apart. The records show the auricular contraction preceding the ventricular. The period of a complete cycle is much longer in tortoise. The total period is 34 dot-intervals, or 1·7 seconds. In the particular specimen of frog the total period is represented by 14 dot-intervals or 0·7 second, while in the fish it is 16 dot-intervals or 0·8 second. Again in tortoise after the commencement of the less pronounced systolic contraction of the auricle, the contractile wave reached the ventricle in the course of 0·6 second, whereas in the frog and in the fish the interval is only 0·2 second, or one-third that in tortoise. The records show other characteristic differ-

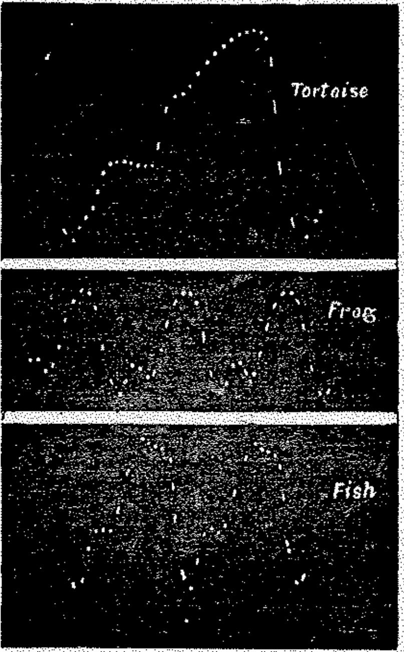

Fig. 121. Characteristic cardiograms of tortoise, frog and fish. The successive dot-intervals represent 0·05 sec.

ences and give very striking visual demonstration of the relative activity at different phases of the pulsation. When the activity is very great the markings are very wide apart and the dots are lengthened into dashes; with slowing down of activity the dots become thin and drawn close together (fig. 121). Under the action of depressing agents the post-diastolic pause becomes greatly prolonged.

Similarity of Rhythmic Mechanism in Animal and Plant

I have demonstrated elsewhere the remarkable similarity of rhythmic mechanism in animal and plant. In both, lowering of temperature slows down the pulsation culminating in an arrest. Rise of temperature up to an optimum, on the other hand, enhances the frequency. Diminution of internal pressure causes an arrest in both. The rhythmic tissue in animal and plant, has a long refractory period. In both, application of external stimulus has no effect during systolic phase of contraction, whereas an extra-pulsation is produced by stimulus during the diastolic phase of expansion.

The effect of drugs is often remarkably similar in the two cases. Dilute solution of potassium bromide causes a depression of cardiac pulsation; this depression is removed by the physiological antagonism produced by certain drugs.

I have recently been engaged in investigating the action of various medicinal plants of India on the activity of the animal heart. Among these I find that a heart in a state of depression is greatly stimulated by extracts of *Abroma augusta.*

In the following record the normal heart-beat of fish is seen to be greatly depressed by KBr solution. Subsequent application of Abroma extract caused a remarkable revival of activity (fig. 122). Even more remarkable are the exactly parallel reactions of K Br and Abroma on rhythmic pulsations of Desmodium gyrans (Fig. 123).

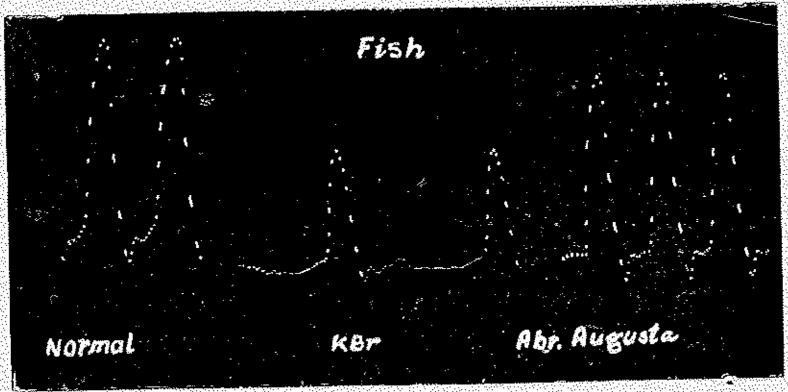

Fig. 122. Effects of depressant and stimulant on Cardiac pulsation of fish. The first series represents normal pulsation; the second, depression under KBr solution; the third exhibits revival by Abroma extract.

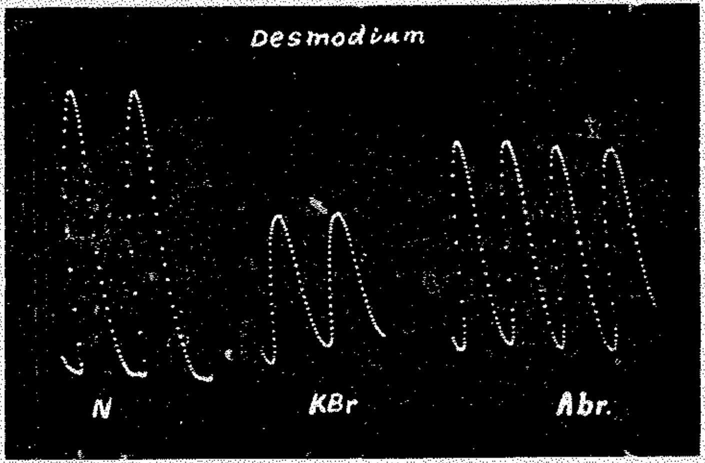

Fig. 123. Effects parallel to the above in pulsations of Desmodium plant.

XXIX

GENERAL SUMMARY

The investigations described in the present volume are on: A, the optical properties of electric waves; B, the characteristics of metallic-contact receivers which respond to electric radiation, either by a diminution or an increase of resistance; C, different types of molecular receivers which respond to diverse modes of stimulation; D, the similarity of response of inorganic and living substances; E, the physiological response of plants; and F, the identity of physiological mechanism in animal and plant.

A. Optical Properties of Electric Waves

Electric waves of great length curl round corners; accurate angular measurements are thus rendered impossible. The difficulty has been obviated by securing a narrow beam of electric radiation of relatively short length.

1. *Complete Electric Wave Apparatus*

The Radiator.—Electric radiation is produced by a single spark between two hemispheres and an interposed small sphere of platinum, the wave-length being reduced to about 5 mm. The sparking coil and battery are enclosed in a small double-walled metallic box with a tube for the passage of the electric beam. Magnetic disturbance due to the make and break of the sparking coil, was found to affect the receiver; the magnetic

disturbance was eliminated by making the inner box of soft iron which acted as a magnetic screen.

The Receiver.—A satisfactory form of receiver was constructed of steel or of nickel; a single point contact receiver made of steel, nickel, aluminium or magnesium is also found to be highly sensitive and reliable. The sensitiveness can be exalted to any degree desirable by adjustment of electromotive force acting on the circuit. Angular measurements are made with the spectrometer circle (p. 87).

2. *Selective absorption*

The transparency or opacity of various substances, brick, wood, pitch and others as well as strata of different liquids and solutions can easily be demonstrated by interposing them on the path of electric beam. Water is opaque on account of absorption of radiation; liquid air is, on the other hand, quite transparent. Sheets of metal do not transmit, but reflect the beam according to laws of reflection. A long trough filled with irregularly shaped pieces of pitch is opaque on account of multiplicity of reflection and refraction. It becomes more or less transparent when partial homogeneity is restored by pouring in kerosene (p. 89).

3. *Determination of Index of Refraction*

The prism method is quite unsuitable for exact determination of the index for the electric ray. Accurate results have, however, been obtained by the method of total reflection. The rotation of two semi-cylinders separated by parallel air-space, produce a sudden extinction of the image at the critical angle. The index of refraction of glass for the electric ray is found to be

2·04, which is much higher than the index 1·53 for the sodium light. The index for sulphur is 1·73 (pp. 21, 31).

4. *Influence of Thickness of Air-space on Total Reflection*

On account of extreme shortness of wave-length of the visible rays, the thinnest air-film produces total reflection at the critical angle. The case is, however, different with comparatively greater wave-length of electric radiation. The critical thickness of air-space is modified by the angle of incidence and by the wave-length. When a cube of glass is interposed between the radiator and receiver placed opposite to each other, the radiation striking one face perpendicularly is transmitted across the opposite without deviation and causes response of the receiver. On cutting the cube across a diagonal, two right-angled isosceles prisms are obtained. When the two prisms are separated slightly, keeping the two hypoteneuses parallel, thus securing parallel air-space, the incident radiation is found divided into two complementary portions, of which one is transmitted and the other reflected by the air-film at right angles to the incident ray. When the thickness of air-space is reduced to about 0·3 mm., there is a complete transmission and no reflection. The two prisms in spite of the breach due to the air-space, are electro-optically continuous. A greater separation of the two prisms increases the reflected, at the expense of the transmitted portion; and at a certain critical thickness, there is no transmission but total reflection. If a thin piece of cardboard or any other refracting substance be next interposed, a portion of the radiation becomes transmitted, necessitating further separation of the prisms to reduce the transmitted portion to zero. This offers

a means of determination of the index of refraction of plates of different substances (p. 44).

5. *Double-refraction and Polarisation*

The shortness of wave-length of electric radiation has enabled investigations on the polarising action of even small crystals. The polariser and analyser are made of fine wire gratings; they can also be made of a number of crystals such as Nemalite, Chrysotile, Serpentine and Epidote. The most perfect polariser and analyser are constructed of jute-fibres or of a book, both of which produce complete polarisation of the electric ray. Crystals of tetragonal, orthorhombic, hexagonal, monoclinic and triclinic systems produce double refraction and polarisation. Locks of human hair and vegetable fibres also produce polarisation (p. 96).

6. *Double refraction by strained dielectric*

Various stratified rocks exhibit very strong double refraction when the plane of stratification producing polarisation, is inclined at 45° to the crossed polariser and analyser, there being no effect when this plane is parallel to either the polariser or the analyser. Unannealed glass and ebonite also produce double refraction and polarisation of the electric ray (p. 95).

7. *Double absorption and double conductivity*

Certain crystals like Nemalite, Chrysotile and Epidote exhibit selective transparency to polarised radiation; these are transparent in one direction but opaque in a direction which is perpendicular to the first. Complete polarisation is due to their property of double absorption. Investigations showed that they also exhibit unequal electric conductivity in the two directions and that the direction of maximum conductivity is also the direction of maximum absorption. Electric vibrations perpendicular to the direction of maximum conductivity are thus alone transmitted, the emergent beam being thus completely polarised (p. 75).

8. *The Production of a "Dark Cross"*

The interposition of a circular structure like that of a disc of rolled paper on the path of polarised electric radiation is found to project a dark cross into space, the outline of which can be definitely found by means of the exploring detector. The production of a dark cross can also be demonstrated by woody stems with concentric rings as also by ringed concretion of flint round a central nodule. Stalactite also gives similar results (p. 115).

9. *Rotation of Plane of Polarisation*

Right handed and left handed rotations of the plane of polarisation are produced by oppositely twisted jute elements. The electro-optic analogues of two varieties of sugar, dextrose and levulose, were thus obtained. An apparently inactive variety was produced by a mixture of equal numbers of positive and negative elements (p. 109).

B. THE CHARACTERISTICS OF METALLIC-CONTACT RECEIVERS

The systematic study of effect of electric waves on contact-resistance of various metals and metalloids showed certain characteristic differences.

1. *Positive and negative classes of substance*

In regard to the variation of resistance induced by electric waves, it is found that substances could be divided into two classes positive and negative. The positive represented by Iron, Magnesium, and others, characteristically exhibits a diminution of resistance; the negative (Potassium, Arsenic, etc.) exhibits on the other hand, an increase of resistance. An intermediate class is found in Silver which under different molecular modifications, exhibits either a diminution or an increase of resistance. Some of these substances, moreover, exhibit an automatic recovery on the cessation of electric radiation (p. 125). The increase of resistance induced by electric radiation and automatic recovery prove that the theory of 'coherence' is inadequate in explanation of the phenomenon. The induced variation of resistance positive or negative, increases with the intensity of radiation. Under continued radiation a maximum effect is produced; there is now a balance between conductivity distortion and force of restoration, recovery becoming complete on the cessation of radiation. These and other facts prove that radiation induces a molecular change of an allotropic character, and that the variation of conductivity is an expression of the induced molecular change (p. 161).

2. *Molecular Recovery*

When the range of electric elasticity is not narrow, the substance exhibits an automatic recovery. In other substances the recovery is more or less prolonged. Even in such cases the recovery is hastened by molecular vibration produced by a mechanical tap, or by heat. These restore the sensitive substances from the state of induced molecular strain (attended by change of conductivity) to their original condition and original conductivity. In the positive class, a tap or application of heat restores the substance to original condition by an increase of resistance; in the negative class the restoration is by a diminution of resistance to the normal (p. 158).

3. *Characteristic Cyclic curves under E. M. Variation*

The conductivity change is produced not only under very rapid electromotive variation by electric waves, but also by a comparatively slow electric variation. Electric conduction in metallic particles sensitive to electric radiation does not obey Ohm's Law. The conductivity is not constant and independent of E. M. F. but varies with it. The two classes of substances, positive and negative can be discriminated from each other by their characteristic curves under cyclic electromotive variation.

The characteristic curve is obtained by recording the variation of the electric current produced under increasing E. M. F. For surface contact of positive class of substance like iron, the curve is concave to the axis of current. Under cyclic E. M. F. variation, the forward and return curves do not coincide; there is a hysteresis. The greater is the range of E. M. F. the greater is the area enclosed. The residual effect can be dissipated by mechanical vibration.

In the negative class of substance like potassium, the curve is of an opposite character being *convex* to the axis of the current. Increase of E. M. F. produces an actual diminution of current or an increase of resistance. This class exhibits an increase of resistance under electric radiation (p. 251).

C. DIFFERENT TYPES OF MOLECULAR RECEIVERS

External disturbances or stimuli impinging on a substance induce a molecular upset, the effectiveness of the stimulus depending on the rapidity of the onset of the disturbance. The molecular upset is attended by changes induced in the properties of the substance. The most sensitive means for its detection is electrical: by the method of conductivity or of electromotive variation (p. 170).

Stimulation of the substance can be produced by electric radiation, by visible light, and by mechanical vibration.

1. *Continuity of Effect of Electric Radiation and Light*

Method of conductivity variation.—This is specially well suited for studying the effect of electric radiation on discontinuous particles; for since the action of radiation is one of surface layer, the larger the area, the more pronounced is the effect, and in loose particles the effective surface is greatly enlarged. The effective total resistance of the particles, moreover, is due to the resistances of surface contacts; any change in the property of the surface layer therefore causes a great variation of the total resistance. There are two classes of substance of which the positive responds by a diminution and the negative by an increase of resistance (p. 135). The effect of radiation is annulled by mechanical vibration. The continuity of effect of electric radiation and light is seen in the galena receiver which responds to both visible and invisible lights by a diminution of resistance (p. 269).

Method of electromotive variation.—A difference of electromotive force is generated between two areas of the same substance, when one is exposed and the other shielded from electric or visible radiation. The characteristics of response to electric radiation and light under diverse conditions are found to be essentially similar (p. 187).

2. *Response to Mechanical Vibration*

Rapid mechanical vibration, also induces an electromotive variation between the stimulated and unstimulated portions of the same wire (p. 195). The response to mechanical stimulation is found to be of opposite sign to that under light as demonstrated by alternately subjecting one of the two wires of a strain cell to the two modes of stimulation. It is moreover possible to exactly balance the effect of one by that of the other, a slight increase or decrease of either producing an immediate upset of the balance in one direction or its opposite (p. 206).

3. *Molecular Response common to Electric Radiation, Light and Mechanical Vibration*

1. The molecular effect induced by stimulus can be detected in all cases by the methods of conductivity or of electromotive variation.

2. Substances exhibit quick recovery after moderate stimulation; the recovery becomes protracted, in consequence of overstrain caused by intense stimulation.

3. Response is modified by the previous history of the substance and by changes of the environment. Slight rise of temperature and annealing ensures an increased sensitiveness and quick recovery.

4. The ascending portion of the curve of response is abrupt, whereas the fall during recovery is at first rapid and then comparatively slow; the curve of recovery is thus convex to the abscissa which represents time.

5. Under increasing intensity of stimulation, the amplitude of response undergoes an increase which reaches a limit.

6. Sub-minimal stimulus induces a response of opposite sign to that under moderate stimulation.

7. Under rapidly succeeding stimuli, the individual responses become fused; the curve rises to a maximum, when the force of restitution balances the force of distortion due to stimulation.

8. Under prolonged stimulation, the response tends to become reversed; during this process the reversal may become recurrent.

4. *The Strain Theory of Photographic Action*

The photographic effect of light is detected in a few cases only, when the induced change happens to be visible or is rendered visible on development; the image often disappears on account of self-recovery during darkness. The changes induced can, however, be followed in all its phases in the resulting curve of electric response. In this curve the period of overcoming molecular inertia corresponds to the induction period of photographic action; the automatic recovery explains relapse of the impressed image.

This impression can be rendered more permanent by molecular overstrain under strong and long-continued action of light, the recovery from overstrain being thus greatly prolonged. The fact that molecular strain induced by light is universal, is shown by images produced not merely on photographic plates, but also on sheets of ordinary metals (p. 213). Molecular impression produced in other ways than by light is seen in the inductoscripts and in the development of pressure marks.

Recurrent photographic reversals are produced under continued action of light similar to those under continuous mechanical stimulation (p. 215).

Owing to tendency towards self-recovery, the resulting effect does not solely depend on the total quantity of incident light, but also on the time-rate of illumination. Hence for the same duration of exposure, the photographic effects of intermittent and continuous illuminations are not the same (p. 217).

D. THE SIMILARITY OF RESPONSE OF INORGANIC AND LIVING SUBSTANCES

A molecular upset is produced in inorganic substances by the impact of stimuli, electrical or mechanical. The response is recorded by methods of conductivity and electromotive variations.

In inorganic receivers for electric radiation, continuous stimulation induces fatigue which is removed after a period of rest. Prolonged rest, however, makes the receiver inert, and the lost responsivity is then only restored after a period of stimulation (p. 253). These characteristics are similar to those in the response of living substance.

Successive stimuli of equal intensity give rise to uniform inorganic responses. Superposition of stimuli causes incomplete or complete "tetanus" according to slow or quick frequency of stimulation (p. 256).

Certain chemical substances produce a great enhancement in the amplitude of response; these act as stimulants in inducing an increase of excitability (p. 274). Others produce a depression. The variation of excitability induced by various chemical substances, or different doses of the same substance can be detected by the Electric Comparator (p. 282). Slight differences of physico-chemical change in the same piece of metal are detected and recorded by the Electro-molecular Explorer (p. 287).

The effect of an identical chemical agent is modified by the dose of application, a minute dose often producing a reaction opposite to that of a large dose (p. 301). Poisons like oxalic acid cause a molecular arrest and 'kill' the response of metals (p. 303).

E. THE PHYSIOLOGICAL RESPONSE OF PLANT

Among the manifestations in the life of the plant may be mentioned its irritability for response to external stimulation, its growth and its power of storing energy supplied by the environment.

1. *Electrical Response of ordinary Plants*

The power of response in plants has generally been regarded as confined to the sensitives like *Mimosa pudica*. Experimental investigations are described which prove that all plants and their different organs are fully sensitive, and that the characteristic electric response by induced galvanometric negativity given by them is in every way similar to the electric response of animal tissues (p. 309).

Successive equal stimulations give rise to uniform responses. Shortening of the intervening period of stimulation brings about fatigue, which is removed after a suitable period of rest. Stimulus singly ineffective becomes effective by summation of several. The amplitude of response increases with the intensity of stimulus till a limit is reached. Anæsthetics induce a depression of excitability. A large dose of chloroform and poisonous substances produce a permanent abolition of response with the death of the plant (p. 315). The response is also abolished when the plant is scalded to death (p. 314). The fatal temperature for the plant is about 60° C.

2. *Response of Plant to the Stimulus of Light*

The plant responds to the stimulus of light by contraction on account of which the directly stimulated side of a stem becomes concave seen in the positive heliotropic curvature of stems. The normal electromotive response under light is by an induced change of galvanometric negativity. I succeeded in devising another method by which the excitatory change of the plant-tissue is detected by a diminution of its electrical resistance. The most sensitive device for this purpose is the Quadrant Method which records response to light of so excessively short a duration as that emitted by a single spark (p. 320).

The amplitude of response, by resistivity variation, increases with the intensity light. Very dilute vapour of ether increases the excitability as demonstrated by the enhanced amplitude of response. Strong dose of chloroform, on the other hand, causes depression and death as indicated by gradual diminution and final abolition of response.

3. *The Vegetable Photo-electric Cell*

A very sensitive method of record of the action of light by the induced electromotive variation of galvanometric negativity is afforded by the photo-electric cell in which two similar leaves, immersed in an electrolyte, form the voltaic elements. There is no current in the cell when it is kept in the dark, but exposure of one of the two leaves gives rise to a responsive current. The amplitude of response increases with the intensity and duration of exposure to light. An abnormal positive response occurs when the physiological vigour of the specimen is feeble and below the normal.

In the green leaves two opposite reactions are simultaneously induced under the action of light; of these the A-reaction is associated with the building up process and storage of energy by assimilation; the D-reaction of break-down and expenditure of energy occurs under excitatory action of stimulus. The A-effect is often masked by the predominant D-reaction; the existence of A is demonstrated by the positive electric response exhibited by actively assimilating plants like Hydrilla; it is also shown as an after-effect on the cessation of stimulus (p. 330).

4. *Automatic Record of Response of the Photosynthetic Organ*

The living plant is in a state of unceasing activity, absorbing and storing energy from without, setting free and dissipating it from within. The expenditure of energy may be manifested in movement, or it may not be externally perceptible, being employed in working the internal mechanism of the body—such, for instance, as the distribution of water, which as I have shown elsewhere* involves a considerable expenditure of energy. The fundamental importance of photosynthesis is, that it is the process by which the plant absorbs the energy it requires, the radiant energy of sunlight, and stores it in the form of latent or potential energy in the process. The energy so stored can readily be set free again and become kinetic by the chemical decomposition of the organic substances, manifesting itself in heat, electric current or movement.

All these changes are effected by the living protoplasm and are the expressions of its physico-chemical reactions. This is made clear by the observation that all the various manifestations of them that have been made accessible to investigation are affected in a similar manner by a given stimulus or change in internal or external conditions.

Automatic Recorder for Photosynthesis.—The estimation of the activity of photosynthesis with water plants from the rate of evolution of oxygen is direct and requires no prolonged chemical analysis. The automatic record by the Electro-magnetic Writer of successive bubbles representing equal volumes of pure oxygen eliminates all personal error of observation. The method is so sensitive that records may be obtained from which it is possible to estimate the formation of quantities of carbohydrate as small as the millionth of a gramme (p. 333).

The automatic method of record that has been described, can also be utilised in physico-chemical investigations, such as the determination of the rate of evolution of a gas under controlled conditions of temperature, of concentration, of intensity of light, of catalytic agents and others, either separately or in combination.

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* Physiology of the Ascent of Sap, 1922.

5. *Hourly variation of photosynthetic activity*

In the median range of the photosynthetic curve the increase of activity is proportional to the intensity of light. The latter is determined by the Self-recording Radiograph (p. 338). As regards the effect of rise of temperature, the increase of photosynthetic activity is uniform in the median range of temperature variation, there being an abrupt decline beyond the optimum. The combined effects of the factors of variation of light and temperature, explain the hourly variation of photosynthetic activity which is at its maximum at about 1 p.m. (p. 334).

6. *Effect of infinitesimal traces of chemical substances*

Investigations on the effect of infinitesimal traces of certain chemical substances show that they produce a very great increase in the activity of assimilation. The demonstration of this is of special interest since it enables us to understand the effect of infinitesimal quantities of vitamin on general assimilation and of hormones on physiological reaction.

The effect of minute quantity of formaldehyde in enhancing the activity is of special significance in regard to the possible formation of formaldehyde as the first product of photosynthesis. This substance is toxic only in a strong dose; before there could be any great accumulation of this substance in the cells it would have become polymerised into carbohydrate.

7. *Efficiency of photosynthetic storage of energy*

The estimates hitherto obtained indicate generally a very low efficiency; the experimental methods employed in this determination have been defective from absence of means for the exact measurement of the energy absorbed, and the energy stored in photosynthesis. The difficulties have been obviated by the new methods devised for the purpose. The energy absorbed is found by the Calorimetric method. The accuracy of the calorimetric determination was tested independently by results obtained with the highly sensitive Magnetic Radiometer (p. 360). The energy stored was simultaneously found from the volume of oxygen given out by the plant, the carbohydrate factor of which had been very carefully determined. The photosynthetic efficiency of the leaves of Hydrilla is fairly high, being about 7·4 per cent. (p. 336).

8. *The activity of growth*

The essential difficulty of the investigation arises from the extraordinary slowness of growth, the average rate of which is about $\frac{1}{100,000}$ inch per second, a length which is half that of a single wave of sodium light. Even with the magnifying growth recorders hitherto employed, it takes a very long time to detect and measure its rate. For accurate investigations on the effect of a given agent on growth, it is necessary to keep all other variable conditions, such as light and warmth, strictly constant during the whole period of the experiment. We can keep these conditions absolutely constant for only a few minutes at a time. Experiments which require several hours for their completion are, therefore, subject to serious errors which vitiate the results.

The only satisfactory method is one that reduces the period of the experiment to a few minutes; that, however, necessitates the devising of an apparatus for exceptionally high magnification, and for the automatic record of the magnified rate of growth.

The High Magnification Crescograph gives automatic record of growth under a magnification of ten thousand times (p. 348). With this it is possible to obtain growth-record in a time shorter than a second and determine its absolute rate, which in S. Kysoor is 0·95 μ per second, where μ represents micron or 0·001 mm.

Effect of variation of temperature.—The effect of rise of temperature in acceleration of growth can be determined in a few minutes (p. 349). It is thus possible to make accurate determinations of the optimum temperature for maximum growth and the minimum temperature for the arrest of activity.

Effect of Chemical agents.—The effect of manures, anaesthetics, drugs and poisons can be similarly determined in a few minutes and with unprecedented accuracy. The effect of a chemical agent is found to be modified by the dose of application (p. 351).

The Balanced Crescograph.—A still higher sensitiveness in recording the slightest change of growth was secured by the method of balance in which by a clockwork device, the plant is made to descend exactly at the same rate at which the growing tip of the plant was rising (p. 352). The rate of growth is thus accurately compensated and the recorder dots a horizontal line of balanced growth. The minutest change induced in the rate of growth by the environment is at once indicated by the upset of the balance shown by the up and down movements of the curve. The method is so extremely sensitive that it detects and records variations in the rate of growth so excessively minute as $\frac{1}{1500}$ millionth of an inch per second.

Wireless waves and growth.—The results obtained by the Balanced Crescograph prove that electric waves used in signalling through space are effective in modifying the rate of growth. The perceptive range of the plant is far greater than ours ; it not only perceives but also responds to different rays of the vast ethereal spectrum.

Opposite reactions under feeble and strong stimulation.—This appears to be a universal phenomenon, characteristic of response of both inorganic and living substances under diverse modes of stimulation. This is seen in the responses of inorganic matter to electric radiation. In the positive class, *e.g.* Osmium in which the response to moderate stimulation is by a diminution of resistance, a subminimal stimulus induces a response by an increase of resistance (p. 137). Similar opposite responses under moderate and feeble stimulation are also exhibited by negative class of substance represented by Arsenic (p. 137). The electromotive response of metallic wires under mechanical stimulation also exhibits this characteristic (p. 204). A short-lived negative twitch is often observed preceding the normal response designated as positive. This is due to the fact that it takes a short time before the responding substance can absorb the whole amount of incident stimulus, the first moiety absorbed being sub-minimal (p. 181). This characteristic effect is exhibited not only by electro-magnetic receivers (p. 189) but also by photo-electric cells responding to light (p. 190) and by strain cells under mechanical stimulation (p. 204).

In plants also similar reactions are observed. This is seen in the opposite effects of feeble and strong intensity of electric waves in enhancement and retardation of growth respectively (p. 355).

Parallel effects are also observed in regard to chemical stimulation of both inorganic and on living matter. The same reagent which in large doses causes a depression of excitability and abolition of response in metals, induces, on the other hand, a great enhancement of response when the dose is sufficiently minute (p. 301).

In the living plant, poisons produce death and permanent abolition of response. In minute doses, however, they induce a great enhancement of vital activity thus acting as a highly efficient stimulant in promotion of growth (p. 351).

The Magnetic Crescograph.—The magnification is very greatly increased by the Magnetic Crescograph which produces a magnification of about 50 million times; this order of magnification would lengthen a single wave of sodium light to 2,500 cm. (p. 357).

The Magnetic Radiometer.—This enables comparison of energy of every ray in the solar spectrum (p. 362).

F. IDENTITY OF PHYSIOLOGICAL MECHANISM IN PLANT AND ANIMAL

A continuity of response having been established between the responses of inorganic matter on the one hand and living plants on the other, inquiry was continued to find out whether the fundamental physiological mechanisms were similar in plant and in animal life. The plant world affords an unique opportunity for studying the changes by which a simple and primitive organ becomes gradually transformed into one of greater complexity. The evolutionary process has been active not only in morphological differentiation, that is, in the development of new forms, but also in physiological differentiation, that is, in the development of specialised mechanisms for the performance of the various vital functions. There still exists a long prevalent idea that physiological mechanisms of animals and plants are fundamentally different. The evidence afforded by results of experimental investigations show that this idea is unfounded.

The most important characteristics of certain animal tissues are (1) *contractility* on account of which rapid movement is produced by muscular organ ; (2) *conductivity* or power of transmitting excitation to a distance and (3) *rhythmicity* or so called spontaneous movements.

Muscular organ in plants.—The functional similarity between the two contractile organs, pulvinus and muscle, is not confined to the manifestation of outward movement, but can be traced to the ultimate protoplasmic mechanism. There are three types of contractile organs distinguished by their rapidity of reaction. The wing-muscle of a bird of prey like the falcon is very active ; that of the goose is less active, while the muscle of the domestic fowl is almost inactive, its power of flight having been practically lost. The activity of animal muscle is found to be dependent on the presence and relative distribution of an active substance.

In the leaves of plants there are similarly three types of motor organ—active, semi-active and inactive. The first is exemplified by Mimosa pudica, the second by Neptunia oleracea ; and the third by the pulvinus of Phaseolus in which the movement is very feeble and extremely sluggish. By means of selective staining I succeeded in producing a sharp differentiation of the

actively contractile from other inactive cells. In Mimosa the active substance is present in great abundance ; in Neptunia the particular substance is quantitatively less and scattered. In the inactive Phaseolus the active substance is altogether absent.* The pulvinus of Mimosa may thus be regarded as functionally equivalent to an active animal muscle.

Nervous tissue in plants.—Some of the crucial tests for discrimination of nervous impulse are (1) that excitation is initiated for transmission by the characteristic polar action of a constant electric current ; (2) that the velocity of transmission is increased within limits, by a rise of temperature ; (3) that the transmission can be arrested temporarily or permanently by various physiological blocks. The conducting power is temporarily arrested during the passage of an electric current in a portion of the conducting tissue through which the impulse is being transmitted, the block being removed on the stoppage of the current ; (4) that the conducting power is permanently abolished by poisonous solutions. The results of application of these crucial tests offer conclusive proof that the conduction in the plant is a phenomenon of protoplasmic excitation as in the nerve of the animal.

The velocity of transmission in plants is accurately determined by the Resonant Recorder by which time-intervals as short as $\frac{1}{200}$ sec. can be recorded. The velocity of transmission is sometimes as high as 400 mm. per second. It is slower than the nervous impulse in higher, but quicker than in lower animals (p. 369).

Rhythmic tissue.—I have demonstrated elsewhere the remarkable similarity of rhythmic mechanism in animal and plant.* In both, lowering of temperature slows down the pulsation culminating in an arrest. Rise of temperature to an optimum, on the other hand, enhances the frequency. Diminution of internal pressure causes a similar arrest in both. The rhythmic tissues in animal and plant have a long refractory period. In both, application of external stimulus has no effect during systolic phase of contraction, whereas an extra-pulsation is produced by stimulus during the diastolic phase of expansion (p. 372).

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* Plant Autographs and their Revelations, 1927.

Records of rhythmic cardiac pulsation were obtained with Resonant Cardiograph which gives the most accurate record of the different rates of movement at different phases of the cardiac cycle (p. 371).

The effects of certain drugs are found to be remarkably similar on rhythmic tissues in animal and plant. Certain drugs thus cause in both a great depression of activity; subsequent application of a particular drug then causes a marked revival of activity.

A considerable portion of this volume deals with the optical properties of electric waves, the study of which has been facilitated by devices for the production of short waves and reliable means for their detection. Results have been obtained which show that electric radiation produces allotropic modification in matter analogous to those by visible light. The most unexpected results are those which demonstrate a continuity of response in the Living and Non-living.

The intricate mechanism of life can only be elucidated by extension of our power of investigation, often in the realm of the invisible. It is only from facts so

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* Irritability of Plants, 1913.

ascertained that a fully satisfactory theory can be established in regard to diverse activities of life; it is not improbable that these will some day be ultimately traced to physico-chemical reactions.

Physics in a larger sense includes investigations on the reactions of matter, both inorganic and living. The methods of investigation are identical in the two cases. The various appliances described, the very high magnification and record of imperceptible movements, the automatic record of extremely short intervals of time and the rate of reaction, the measurement of energy of different rays of the solar spectrum and of the transformation and storage of the energy by the photosynthetic organ—these and others will also be found of value in the advancement of purely physical and physico-chemical investigations.

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